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SABELLA AND AMPHITRITE

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ON TYPICAL BRITISH MARINE PLANTS & ANIMALS

EDITED BY
R. J. DANIEL, D.Sc.

XXXIII.

POMATOCEROS
SABELLA AND AMPHITRITE

BY

JOAN G. THOMAS, B.Sc.
BIRKBECK COLLEGE, UNIVERSITY OF LONDON

(With 11 Plates)

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EDITOR'S PREFACE

THE Liverpool Marine Biology Committee was constituted in 1885, with the object of investigating the fauna and flora of the Irish Sea.

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No. XXXIII. POMATOCEROS
SABELLA AND AMPHITRITE

BY

JOAN G. THOMAS, B.Sc.
Birkbeck College, University of London

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INTRODUCTION

The Polychaeta, which form one of the main divisions of the Chaetopoda, are arranged in two groups—the Errant Polychaetes and the Sedentary Polychaetes. The Sedentary Polychaetes may be sub-divided into six superfamilies—the Spioniformia, Terebelliformia, Capitelliformia, Scoleciformia, Sabelliformia and Hermelliformia. Those dealt with in this memoir belong to the Terebelliformia and Sabelliformia and the families which these contain are shown in the following table :—

- *Superfamily* 1. Spioniformia.
- *Superfamily* 2. Terebelliformia.
    - *Family* a. Amphictenidae.
    - *Family* b. Ampharetidae.
    - *Family* c. Terebellidae.
- *Superfamily* 3. Capitelliformia.
- *Superfamily* 4. Scoleciformia.
- *Superfamily* 5. Sabelliformia.
    - *Family* a. Sabellidae.
    - *Family* b. Serpulidae.
- *Superfamily* 6. Hermelliformia.

The Sabelliformia and Hermelliformia are sometimes grouped together as the Cryptocephala in contrast to the remaining Polychaetes which form the Phanerocephala.

Pomatoceros, of which there is only one species, *P. triqueter* (L.),* belongs to the Serpulidae. *Sabella* is a member of the Sabellidae and is represented in Britain by the single species *S. pavonina* (Savigny).

Amphitrite is one of the Terebellidae : there are five species found in the British Isles :—

A. gracilis (Grube)—2 pairs of gills, 17-19 segments with long chaetae.

A. cirrata (O. F. Müller)—3 pairs of gills, each with a tuft of unbranched filaments, 17 segments with long chaetae.

***The authors of the species found in the Port Erin area are those given by Moore (1937): the others follow Fauvel (1927).**

A. edwardsi (Quatrefages)—3 pairs of branched gills, 17 segments with long chaetae.

A. groenlandica Malmgren—3 pairs of branched gills, 19 segments with long chaetae.

A. johnstoni (Malmgren)—3 pairs of branched gills, 24 segments with long chaetae.

A. johnstoni was chosen for detailed description on account of its fairly frequent occurrence and suitable size for dissection.

The three genera show varying degrees of modification to a tube-dwelling existence, *Pomatoceros* being the most completely adapted and *Amphitrite* the least.

Pomatoceros triqueter is common on all the rocky shores of Britain, extending from above low-water mark to 50 fathoms. The short limy tube, characterised by a crest along its upper surface, is usually attached to a rock, stone, or shell, throughout its length. In very sheltered positions, such as Loch Ine in S.W. Ireland, and also according to Dons (1927), when space is limited, the anterior end of the tube may be free and the crest may be absent in this part. When covered with water the anterior end normally protrudes from the tube, but the rest of the body remains permanently within. If disturbed the worm can retract its whole body some distance down the tube.

Sabella pavonina, which inhabits tubes formed of coarse mud mixed with mucus, is common in many parts of Britain, including Port Erin. Near low-water mark, where the tubes are partially embedded in the mud, they may reach a length of two feet ; in deeper water, where they are not so buried, they are shorter and narrower. As in *Pomatoceros,* only the head of the worm emerges from the tube.

Amphitrite lives in tubes which are usually merely excavations in mud or sand, and do not project above the surface. *A. gracilis* and *A. johnstoni* occur at various localities around the coast of Britain, including the Devonshire coast. The latter species only is found in the Isle of Man, where it has been collected at Port Erin. It is usually accompanied by the commensal *Gattyana cirrosa* at St. Andrews.

A. edwardsi has only been recorded in the south-west of the British Isles, where it is usually found with one of the commensals *Lepidasthenia argus* or *Harmothoë lunulata*.

A. cirrata occurs chiefly on the coasts of northern England and Scotland.

A. groenlandica is found off the coasts of Ireland and in the North Sea.

In the following account, *A. johnstoni* is always referred to unless another species is definitely named.

METHODS

Most of the anatomy of *Pomatoceros* has to be made out from microscopic sections. The worms are small enough to be fixed and cut whole, although the removal of the operculum facilitates sectioning ; alcoholic Bouin or Susa* are suitable fixatives. For general anatomy Azan* is the best stain, while for histology Heidenhain's iron haematoxylin is good. Worms fixed in 70 per cent. alcohol and bisected along the sagittal plane are also helpful when examined through a binocular microscope.

Much of the anatomy of *Sabella* can be made out from dissection, but for details sections are necessary. The same fixatives and stains may be used as for *Pomatoceros*, but only small pieces of worm should be fixed.

Sections of *Amphitrite* are only necessary for the study of the brain and the nerves arising from it and for histology. Alcoholic Bouin is again a suitable fixative. Haematoxylin and eosin give a good stain for anatomical work, and iron haematoxylin for histology.

Pomatoceros will live for a week or more in unaerated water provided any seaweed attached to the pieces of rock is removed. *Sabella* is best kept in aerated water, while for *Amphitrite* aeration is essential.

*** See, e.g., E. Sharpey-Schafer's "Essentials of Histology," 14th Edition.**

POMATOCEROS TRIQUETER

The Tube

The tube is calcareous, but if the calcium carbonate is dissolved in hydrochloric acid, a thin membrane is left, which stains deeply with mucicarmine and is therefore of a mucoid nature. It is always curved, sometimes in more than one direction, and a keel is developed to a varying extent along its upper side (Figs. 1, 2). Anteriorly the keel ends in a point which projects above the opening: the degree of development of this projection appears to vary in different localities, as McIntosh (1923) states that it is sharper in forms from North Uist than in those from St. Andrews.

Dons (1927), who studied the growth of the tube in specimens from the coast of Norway, states that the first formed tube, which is only temporary, has two projections at the posterior end, which are attached to the substratum. The permanent tube is built as a continuation of this temporary one, which in time dissolves; the limit between the two is not easily seen. He found the growth rate to be approximately 1·5 mm. per month, although this of course varied with external conditions, and considered that some of the tubes he found belonged to specimens at least four years old.

The anterior 5 mm. or so of the tube is often much whiter than the rest, with a fairly sharp demarcation between the two. This makes it appear probable that the tube is not secreted continuously, the differences in colour in the older parts having been obliterated. To find whether this discontinuity could be attributed to periods of low temperature, an experiment was performed to ascertain the minimum temperature at which a tube could be secreted, by removing worms from their tubes and keeping them in a differential thermostat. It was found that secretion of calcium carbonate could occur above about 7·0° C. but not below. As the temperature of rock pools and shallow water off Plymouth does not usually fall below 8·2° C. (Atkins, 1919-22), temperature differences alone do not appear to explain the discontinuity.

It seems unlikely that the amount of calcium present in the water is the limiting factor for tube formation because in Potts' experiments (described by Robertson and Pantin, 1938) it was found that a tube was produced at the same rate in artificial sea water containing only half the normal amount of calcium chloride, as in water containing the full amount.

Probably therefore the secretion of calcium carbonate is not dependent on any one external condition but is controlled by the interaction of several factors, of which possibly some only are external.

The tube is not always complete on the attached surface. According to Faouzi (1930-31) it cannot be completed owing to the gap between the two lateral lobes of the collar on the dorsal side, but some specimens have been found in which it was (Fig. 2).

When the tube is rubbed down with sandpaper a series of spaces (Figs. 2, 3, PERF.) is usually seen on each side extending throughout its length ; they are rather irregular in shape, but in transverse sections appear roughly pyramidal, with the base of the pyramid towards the substratum. It is probable that they are left to economise the amount of material used. Similar canals are found in such Serpulids as *Vermiliopsis* and *Pomatostegus* (Fauvel, 1927). In a thin section, the whole tube is seen to be penetrated by fine canals formed as a result of only certain cells of the collar secreting lime.

[*To make a thin section, take a small piece of tube and rub one side down with sandpaper until a flat surface is obtained, as nearly as possible at right-angles to the long axis. Stick this to a slide with Canada balsam and leave it for some days to dry. Then rub the other surface down until a thin section is obtained, wash and cover with more Canada balsam.*]

Sometimes holes are found penetrating the sides of the tube ; they are often fairly regularly arranged, and may possibly be of use for the intake and outlet of water for respiratory purposes, although as they are not found in most tubes it is more likely that they, like the series of spaces within the tube, are merely to economise material.

Occasionally the posterior end of the tube becomes blocked by a calcareous plate (Fig. 4), with holes in it resembling those in the tube. As these plates cannot possibly be formed by the collar, another part of the worm must be able to secrete calcium carbonate on occasion. It is possible that exposure of the posterior end of the worm to a greater quantity of sea water by the breakage promotes secretion in this region.

The direction of growth of a tube of *Pomatoceros* seems to be due to chance as it is not generally correlated with any structural peculiarities of the substratum, and is not apparently determined by light or gravity.

If *Pomatoceros* is removed from its tube it usually begins to make a new one within a few hours : Faouzi (1930-31) described the process, but his description of the initial stages differs somewhat from the following account. The first sign of tube formation is the whitish appearance of the middle of the ventral collar fold ; this is sometimes visible in a worm just removed from its tube. A limy plate is then formed in each lateral collar fold, and these three plates then join to form a spur-shaped piece, which gradually increases in size.

Pomatoceros never regenerates a complete tube, probably because of the movement of the worm which prevents successive spur-shaped pieces from fitting together correctly, and which also prevents the tube from being fused to the substratum.

Potts (Robertson and Pantin, 1938) considered that the calcium for tube-building was obtained directly from the sea water ; his evidence for this was that worms removed to calcium-free sea water immediately after feeding, cannot produce a tube, and that there are no special organs which might be used for storing calcium. The blood does not seem to be a storage place, since worms which lose much blood on being removed from their tubes can still form a new one. I have collected further evidence which points to the same conclusion : worms in which the posterior region had been removed as far as the third thoracic segment, still began to secrete a tube soon after their removal from the original one, while a worm in which the collar had been removed showed no signs of tube formation at the end of seven weeks. Histological preparations to show calcium deposits give no reaction except in the region of the collar.

It may therefore be concluded that the tube is a discontinuous secretion from the collar alone and that material for its formation is obtained directly from the sea water.

General External Appearance

A typical specimen of *Pomatoceros* is from 20-30 mm. long and 2-3 mm. broad : its colour varies from yellow through orange to dark brown or black. The dorsal surface of the worm is always towards the substratum. As in all Serpulids the body is divided into three regions—prostomium, thorax and abdomen.

The *prostomium* is minute and bears the branchial crown, consisting of two outgrowths which branch anteriorly into numerous filaments (Fig. 5, BR.F.). These latter may be blue, brown or occasionally bright pink in colour, with patches of white ; they are described in detail later. At the anterior end of the prostomium is the opening of the dorsal pit (Fig. 18, D.P.)—a small backward inpushing of the body wall. The nephridial opening (Fig. 18, EX.P.) is at the extreme anterior end of this pit.

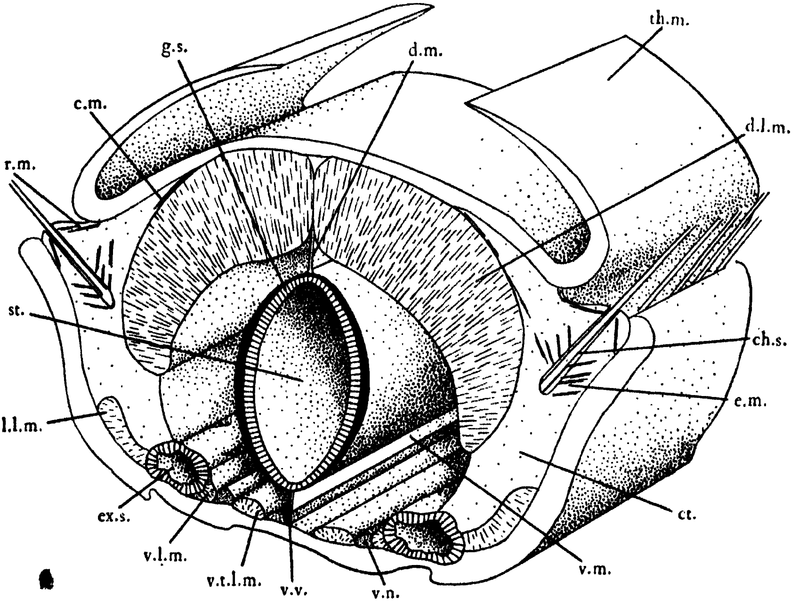
The *thorax* consists of seven segments all bearing chaetae (Fig. 5), which are much reduced in number on the first or peristomial segment.* The first segment bears at its anterior end the collar, a thin fold of skin divided into three parts—a ventral fold and two lateral ones (Fig. 5, V.C.F., L.C.F.)—which are turned back over the tube when the worm is protruding.

Between the ventral and lateral collar folds there is on each side a small lappet (Fig. 5, L.), possibly sensory in function. On each side the lateral lobe of the collar is continuous posteriorly with a thin fold of skin, the thoracic membrane (Fig. 5, TH.M.), which arises from the dorso-lateral surface of the body wall (Text figure 1, TH.M.). These two membranes are applied to the lower surface of the tube during life and thus form a channel between this and the dorsal body wall (Text figure 4). At the posterior end of the thorax the membranes from each side meet ventrally, and end in a lobed or rounded free portion. Meyer (1888) showed the thoracic membrane to be homologous with the dorsal cirri of other Polychaetes.

---

* It is possible that this first segment represents an achaetous peristomium fused with the second body segment as Meyer (1888) described for *Psygmobranchus protensus* (= *Protula protensus*).

The peristomium has no parapodia but bears a few long chaetae in a group on each side. [*To see these turn the lateral collar folds forward.*] The remaining six thoracic segments each bear a pair of parapodia, consisting of a dorsal notopodium and a ventral neuropodium. The notopodia (Fig. 5, NOT.) are narrow dorso-ventrally but elongated antero-posteriorly and bear two rows of long chaetae embedded in a chaetal sac (Text figure 1, CH.S.) ; they lie in depressions at the junction of the thoracic membrane with the body wall (Text figure 1). The neuropodia (Fig. 5, NP.) are low vertical swellings, projecting slightly on their posterior sides, and



Text-Fig. 1

Pomatoceros triqueter. A diagram of a thick transverse section through the region of the stomach.

ch.s., chaetal sac ; *c.m.*, circular muscle ; *ct.*, connective tissue ; *d.l.m.*, dorsal longitudinal muscle ; *d.m.*, dorsal mesentery ; *e.m.*, extensor muscle ; *ex.s.*, excretory sac of nephridium ; *g.s.*, gut sinus ; *l.l.m.*, lateral longitudinal muscle ; *r.m.*, retractor muscle ; *st.*, stomach ; *th.m.*, thoracic membrane ; *v.l.m.*, ventral longitudinal muscle ; *v.m.*, ventral mesentery ; *v.n.*, ventral nerve cord ; *v.t.l.m.*, ventral thoracic longitudinal muscle ; *v.v.*, ventral vessel.

ending dorsally in small flaps which nearly cover the notopodia. Each neuropodium bears a row of small uncini towards its posterior side. The chaetae are described later.

The abdomen consists of from 70-90 segments and is distinguished from the thorax by the absence of a thoracic membrane and by the reversed position of the chaetae—that is the uncini are borne by the notopodia and the long chaetae by the neuropodia (Fig. 5). This inversion is present in all Serpulidae and Sabellidae, but no satisfactory explanation has been found. The first abdominal segment is achaetous. Towards the posterior end the segments become smaller and the last few are often much paler in colour. Near the anus they sometimes lack either long chaetae or uncini. The pygidium, or anal segment, is always achaetous and bears two lateral lobes.

On the ventral side of the abdomen there is a ciliated groove (Fig. 20, V.C.G.) passing from the anus to its anterior end, along which cilia beat in an anterior direction. At the posterior end of the thorax the groove divides into two ciliated tracts, which curve up the right and left sides of the body to the dorsal side. The whole of the dorsal surface of the thorax is ciliated to some extent, but there are two specially well-marked tracts in the angles between the base of the thoracic membrane and the body wall (Text figure 4). The ventral abdominal groove is a necessity for an animal living permanently within a tube for the removal of faeces and reproductive bodies to the exterior, and is found in all Sabelliformia. In worms containing ripe sex products a pair of genital pores is present in all except the posterior segments. They are situated near the ventral groove (Fig. 20, O.OD.).

The Branchial Crown

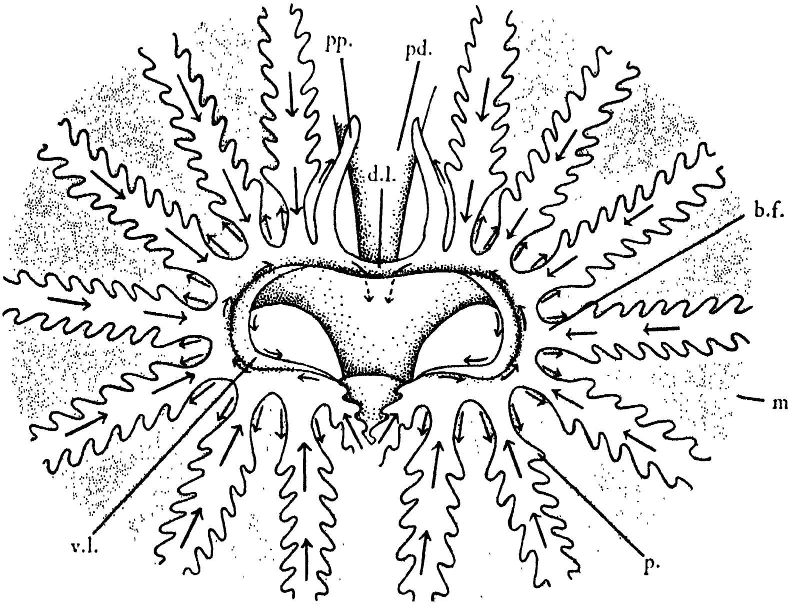
ANATOMY.

The branchial crown consists of two stems borne by the prostomium, which become semi-circular in transverse section anteriorly and then branch out into numerous filaments (Fig. 5, BR.F.), which form the food-collecting apparatus and also assist in respiration. The filaments vary in number but there are usually 14-20 on each side: the most ventral ones are shorter than the rest. The two halves of the branchial crown generally contain the same number ; they are more numerous in large than in small specimens, but there seems no direct correlation between the number of segments and the number of filaments. A thin membrane (Text figure 2, M.) unites those of each side for approximately the posterior quarter of their length. Pruvot (1885), by a study of the nerve supply of the branchial crown, has shown it to be homologous with the palps of other Polychaetes. Except at the distal end each filament bears two rows of pinnules (Text figure 2, P.) arranged in pairs. At the proximal end of each filament the pinnules are replaced by a pair of low longitudinal folds, the basal folds (Text figure 2, B.F.) : these are quite short and each is joined at its base with that of the adjacent filament.

The two halves of the branchial crown are united by the dorsal and ventral lips (Text figure 2, Fig. 18, D.L., V.L.) enclosing a buccal cavity which is crescent-shaped in section. At the points where the dorsal lip joins the two most dorsal basal folds there is given off a long pointed structure grooved on its median side. These structures are always referred to as palps (Text figure 2, PP.). They are not, however, homologous with the entire palps of free-living Polychaetes, but are probably derived from one of the early formed branches of the branchial crown as in the Sabellid *Branchiomma* (Wilson, 1936).

Zeleny (1905) by a study of the development of *Hydroides dianthus*, has shown that the peduncle with its swollen tip the operculum, represents one of the branchial filaments. The peduncle (Figs. 5, 6, 7, PD.) consists of two portions usually triangular in section, the distal bearing at its anterior end a pair of lateral processes (Figs. 5, 6, 7, L.P.) which probably represent pinnules. The operculum (Figs. 5, 6, 7, OP.) (of which the ventral side is usually longer than the dorsal), is very variable in form ; its distal end may be flat (Fig. 5) or slightly concave or may bear two or three projections of varying length (Figs. 6, 7). These differences in the form of the operculum were formerly used as a means of separating *Pomatoceros* into five different species. The cause of the variation is unknown. It is not genetic, since if the operculum is removed the regenerated one is not always of the original type. It does not appear to be due only to external conditions since worms with their opercula removed and kept under similar conditions while regeneration is taking place, form different opercula. McIntosh (1923) on the other hand, found that specimens from N. Uist nearly all had one type of operculum.

From a study of the morphological and ontogenetical evidence, Zeleny (1905) concluded that among the Serpulids, forms with opercula were derived from non-operculate ancestors. Starting from a worm such as *Protula* with no operculum, the next stage would be represented by an animal such as *Salmacina,* with an enlargement at the end of the most dorsal filament on each side; in *Hydroides* there is one large and one very small operculum, and *Pomatoceros* appears to represent the end stage of the series, where the right-hand operculum has been suppressed completely.



TEXT-FIG. 2

Pomatoceros triqueter. A diagram of the branchial crown spread open: the direction of the ciliary currents is indicated by arrows.

b.f., basal fold; *d.l.*, dorsal lip; *m.*, membrane uniting bases of branchial filaments; *p.*, pinnule; *pd.*, peduncle; *pp.*, palp; *v.l.*, ventral lip.

HISTOLOGY.

The *filaments* (Fig. 8) are quadrilateral in transverse section with the longest side outermost and have a groove (Fig. 8, C.G.) running the whole length of the inner surface. Each is bounded by a columnar epithelium (Fig. 8, EP.) resting on a well-defined basement membrane (Fig. 8, B.MB.) ; the cells are tallest in the middle of the outer and lateral faces, becoming low at the outer corners and at the base of the groove. Only the cells of the last are ciliated, the remainder being covered with a thick cuticle (Fig. 8, CU.), which may show striations. The unciliated epithelium consists of cells with lightly staining alveolar cytoplasm, which becomes rather denser at the distal ends, where the nuclei are situated. The cytoplasm of the ciliated cells is more darkly staining and the nuclei are usually in the middle of the cell. The cilia within the groove are small, while those at the summits are much longer and can be seen to arise from a row of basal granules just within the cell. Mucous glands (Fig. 8, M.G.) are present in the ciliated epithelium only. Pigment granules may be present in any of the unciliated cells except those near the groove. These granules are small, somewhat rounded, and insoluble in most fixatives, although their colour may be changed in them.

In each corner of the filament, immediately beneath the basement membrane, is a band of longitudinal muscles, the internal (Fig. 8, I.BR.M.) and external (Fig. 8, E.BR.M.) branchial muscles. Between the two inner muscle bands and also resting on the basement membrane is a nerve (Fig. 8, I.BR.N.) whilst another smaller nerve (Fig. 8, E.BR.N.) runs in each outer corner between the bases of the epithelial cells. In the centre of the filament is a single blood vessel (Fig. 8, BR.V.) lying in a coelomic space (Fig. 8, COE.) ; between this and the muscles or basement membrane is loose connective tissue (Fig. 8, CT.).

The *pinnules* (Fig. 9) are somewhat oval in transverse section, with a shallow ciliated groove on their inner surface. Each is covered by an epithelium of low columnar cells, resting on a basement membrane and covered by a thin cuticle (Fig. 9, CU.). The unciliated cells resemble those of the filaments. The ciliated cells are of two kinds : those in the middle of the groove, which resemble those in the groove of the filament, are usually arranged in three rows and bear short frontal cilia (Fig. 9, F.C.) and there is a row of rather larger cells on each side of these, bearing long latero-frontal cilia (Fig. 9, L.F.C.). In life each of the latter appears as a single cilium, which in fixed material has disintegrated into several separate cilia, joined by short threads to a row of basal granules (Fig. 9, B.G.). Similar compound cilia occur in *Sabella* (Nicol, 1930) and on the gills of *Mytilus* (Carter, 1924). On the outer sides of the cells bearing the latero-frontal cilia is a row of mucous cells (Fig. 9, M.G.). The longitudinal muscles (Fig. 9, L.M.) are situated on the inner side of the basement membrane below the ciliated groove. They are only one or two fibres thick and appear in transverse section as a row of dots. In the centre of the pinnule runs a blood vessel (Fig. 9, P.V.) lying in a coelomic space (Fig. 9, COE.) continuous with that of the filaments.

The *basal folds* are low and are covered with a ciliated epithelium, except on the walls away from the groove, where the cells are unciliated but have a thin cuticle continuous with that on the branchial filaments.

The membrane joining the filaments at their base is composed of two layers of unciliated cuticularised epithelium, resembling that on the filaments. The two layers are separated only by their fused basement membranes.

The *dorsal and ventral lips* (Fig. 18, D.L., V.L.) are composed of an outer and inner epithelium separated by connective tissue in which run numerous small blood vessels (Fig. 18, B.V.), while circular muscle fibres (Fig. 18, C.M.) occur beneath the inner epithelium. In both lips the latter is composed of ciliated cells, which become taller towards the sides and are interspersed with numerous mucous glands (Fig. 18, M.G.); the cells resemble those on the filamentar groove.

The outer epithelium consists of columnar cells, decreasing in height towards the centre of the lips, where they become almost cubical. The cytoplasm of these cells in both dorsal and ventral lips is packed with small spherical granules which stain very darkly with iron haematoxylin and yellow with Azan.

In the central part of the lip some of the cells are ciliated, but those at the sides are covered with a cuticle, which extends as a very thin covering over the outermost ciliated cells in the dorsal lip. In the latter the number of ciliated cells decreases towards the anterior end, particularly in the middle, where, however, the cilia arise in tufts. The number of ciliated cells again decreases anteriorly.

The *palps* (Text figure 2, PP.), like the rest of the branchial crown, are covered with an epithelium of unciliated, ciliated and mucous cells. It is covered with a very thin cuticle, but a basement membrane cannot be distinguished. The unciliated epithelium lines the groove and extends to the dorsal side of the palp; its cells are cubical with granular cytoplasm and nuclei (Fig. 10, N.) situated towards the base. The ciliated epithelium consists of columnar cells with somewhat granular cytoplasm except at the proximal end, where it appears homogeneous and lightly staining. The cilia (Fig. 10, C.) are long except near the groove; towards the dorsal surface they are sparsely distributed. Mucous glands (Fig. 10, M.G.) are present in the outer dorsal epithelium and occasionally on the inner dorsal side. The absence of cilia in the groove is noteworthy but no explanation can be suggested. Blood vessels (Fig. 10, B.V.) are found in the coelomic space occupying the centre of the palp.

The Integument

The Thorax.

The sides and ventral surface of the thorax are covered with an irregular epithelium, immediately below which run many blood vessels (Fig. 18, B.V.). Mucous cells are abundant and some possibly represent the ventral shields which are present in many Serpulids, but absent in *Pomatoceros*. On the dorsal side is a columnar epithelium covered by a cuticle (Fig. 18, CU.) which becomes thinner at the posterior end. Frequently isolated cells are ciliated, the cilia being fairly long and having the same tufted appearance as in the outer epithelium of the ventral lip. This passage of cilia through a thick cuticle is unusual outside the Sabelliformia.

The Abdomen.

The abdomen is covered by an epithelium of short cells, which become larger at the sides of the body around the chaetae, and on each side of the ventral groove. This groove is lined with low cells on which short cilia are sparsely distributed. Mucous glands are numerous on the anterior, posterior and ventral sides of the notopodia, and in the body wall around the anus. Near the latter they also form most of the epithelium lining the groove, but more anteriorly they are restricted to its sides, becoming fewer towards the anterior end.

The Thoracic Membrane.

The thoracic membrane consists of two layers of columnar epithelium (Text figure 1, TH.M.). Sometimes the basement membrane separating them is not visible and the membrane then appears to be formed of an epithelium of long cells with a nucleus at either end. The dorsal epithelium is similar to that of the dorsal body wall but the cells are shorter and the cuticle thinner. Some of these cells bear tufts of cilia, but these are less frequent towards the anterior end and at the extreme posterior end. The ventral epithelium is unciliated, but at its posterior end the cuticle bears some irregular projections. No connective tissue is visible although blood vessels run between the two epithelia.

The Collar.

At their base the lobes of the collar consist of two layers of cuticularised epithelium separated by connective tissue, but towards their free ends this disappears (Fig. 18, V.C.F.) and the epithelial cells become shorter and the cuticle thinner. Blood vessels (Fig. 18, B.V.) are numerous and muscle fibres can be seen running from the attached to the free end.

The Chaetae

The arrangement of the chaetae has already been described. The long bristles (Figs. 13, 14, 15) number around 30 in each thoracic segment except the first where they are much fewer and more slender (Fig. 12). In older specimens the peristomial chaetae may disappear (Fauvel, 1927). The bristles are tapered towards their tips, which point backwards and bear a pair of wings, one being longer than the other. These wings bear faint striations.

In the abdomen there are only 4–8 bristles per segment. The tip is much expanded and bears numerous fine teeth at its edge ; at one side it is drawn out to form a fine curved process (Fig. 16).

The uncini vary in number from 70–130 in each row of a thoracic segment, and from about 30–40 in an abdominal segment, although towards the posterior end they, like the bristles, become reduced in number. Each uncinus (Fig. 11) consists of a broad basal part with strong teeth projecting from it, the last one being somewhat modified, and having a deep hollow beneath it. The number of teeth varies from 7–10.

The long chaetae are used for movement along the tube. The uncini, which are embedded so that only their forwardly directed hooks project, are presumably used chiefly, like the setae of Oligochaetes, for anchoring part of the body to the gelatinous lining of the tube, while another part is expanded by the muscles of the body wall ; thus they assist the bristles in the emergence of the worm from its tube. They may, however, also help in progression along the tube.

The Muscular System

[*The muscular system of* Pomatoceros *is most easily made out from a series of transverse sections.*]

The muscular system differs from that of most Polychaetes in the almost complete absence of oblique muscles. It may be described most conveniently under the following headings :—

1. THE GENERAL BODY MUSCULATURE.

The circular muscle layer (Text figure 1, Fig. 20, C.M.) which is incomplete, lies in most parts beneath the outer epithelium, but between the parapodia of the thorax it forms fairly well-marked vertical bands, separated from the epithelium by connective tissue. The poor development of the circular muscle is correlated with the sedentary mode of life of the worm.

A pair of dorsal longitudinal muscles (Text figure I, Figs. 17, 18, 19, D.L.M.) is present in the thoracic region, but at its posterior end these join to form a large median dorsal longitudinal muscle (Fig. 20, M.D.L.M.). The right dorsal longitudinal muscle is inserted beneath the basement membrane of the epithelium at the base of the branchial crown, while the left goes into the operculum. These muscles are well developed and enable the body of the worm to be retracted quickly into its tube.

The ventral thoracic longitudinal muscles (Text figure I, Fig. 19, V.T.L.M.) form a pair of small bands on the median side of the ventral nerve cords, running above the circular muscles from their anterior insertion beneath the epithelium of the prostomium to their attachment beneath the epithelium of the body wall at the posterior end of the thorax.

The ventral longitudinal muscles (Text figure I, Fig. 20, V.L.M.) run laterally to the ventral nerve cords, lying just below the nephridia in the thorax. Anteriorly they are attached to the connective tissue beneath the ventral epithelium in the second segment. In the abdomen they become larger and form the only longitudinal muscles on the ventral side of the body.

The lateral longitudinal muscles (Text figure I, L.L.M.) extend from the first segment to the posterior end of the nephridia, running near the dorsal side of the latter inside the epithelium of the body wall, to which they are attached at each end.

The oblique muscles (Fig. 17, OB.M.) are represented by a single pair at the anterior end of the nephridia. These, together with the lateral longitudinal and the ventral thoracic longitudinal muscles, probably help in emptying the nephridial sac.

2. THE MUSCLES OF THE BRANCHIAL CROWN.

These consist of three main series :—

A pair of oblique branchial muscles (Figs. 17, 19, O.BR.M.) which are inserted beneath the dorsal epithelium of the body wall where it becomes thickened at the level of the first chaetae. They pass round the outer and on to the ventral side of each half of the branchial crown, ending beneath the epithelium of the latter near the origin of the most ventral filament. By their contraction each half of the branchial crown will be slightly coiled.

The paired internal and external branchial muscles of each filament (Fig. 8, I.BR.M., E.BR.M.) lie in the inner and outer corners respectively. Towards the base of each filament the two inner muscles run together and at the base of the branchial crown those from each filament run posteriorly for a short distance before being inserted on the epithelium of the median side of the base of the branchial crown. The external branchial muscles end posteriorly beneath the outer epithelium at the base of the filament. By their contraction the internal branchial muscles will cause the bending of the individual filaments towards the centre of the crown, while contraction of the external ones will bend them outwards.

The longitudinal muscles of the pinnules (Fig. 9, L.M.) run below the groove and are attached beneath the epithelium of the filament behind its junction with the pinnule. These muscles enable the pinnule to be moved in relation to the filament.

The opercular muscle (Fig. 17, OP.M.) is formed partly from the left dorsal longitudinal muscle and partly from a pair of accessory opercular muscles (A.OP.M.) which split off from the two dorsal longitudinal muscles in the third segment.

3. THE MUSCLES OF THE CHAETAE.

The muscles moving the long chaetae are attached to the chaetal sac in which the latter are situated.

The extensor muscles (Text figure 1, E.M.) are arranged in ill-defined dorsal and ventral groups. In the thorax the former arise from the epithelium of the body wall above the dorsal longitudinal muscle and the latter from the epithelium of the notopodia. In the abdomen, on account of the reversed position of the long chaetae and uncini, the dorsal muscles are inserted on the lateral epithelium and the ventral on the ventral epithelium. In the thorax individual chaetae also have minute muscles attaching them to the wall of the chaetal sac. Protrusion of the chaetae is brought about by the simultaneous contraction of both dorsal and ventral groups of exterior muscles. Movement in a dorsal, ventral, anterior or posterior direction is due chiefly to contraction of the appropriate extensors, possibly aided by very feebly developed muscles attached to the anterior and posterior ends of the thoracic chaetal sacs. [*These latter muscles can only be seen in tangential longitudinal sections.*]

The retractor muscles (Text figure 1, R.M.) pass from the epithelium to the more distal end of the chaetal sac. They are not strongly developed and retraction of the chaetae is probably due chiefly to relaxation of the extensor muscles.

The uncinal muscles consist of a single muscle attached to each uncinus. In the thorax most of these are inserted beneath the epithelium of the anterior face of the neuropodia but some pass to the body wall below the ventral end of the neuropodial ridge. In the abdomen they are similarly attached to the anterior face of the notopodia and the ventral body wall.

4. THE MUSCLES OF THE ALIMENTARY SYSTEM.

These are described under the heading **Alimentary System** (p. 24).

The Coelom

There is a spacious coelom, lying between the body wall and the alimentary canal (Figs. 18, 20, COE.). It is lined by a thin coelomic epithelium except in the first and second segments where this is represented by an irregular layer of vacuolated tissue around the oesophagus (Fig. 18, V.T.).

The coelom is divided by septa (Fig. 18, SEP.) lying between the segments. That of the peristomium is extended posteriorly as two blind pouches running on the median ventral sides of the dorsal longitudinal muscles as far as the third segment. Anteriorly it also sends a pair of extensions passing between the dorsal and ventral roots of the oesophageal connectives (Fig. 19, COE.), giving branches into the filaments (Fig. 8, COE.), and other extensions lying in the connective tissue around the brain.

The coelom is further sub-divided into right and left halves by dorsal and ventral mesenteries (Text figure 1, Fig. 20, D.M., V.M.) extending from the posterior end of the worm as far as the second segment. Here the ventral mesentery ends in the vacuolated tissue round the oesophagus ; the ventral part of the dorsal one is replaced by two strands of connective tissue and the dorsal part forms a loose tissue round the dorsal blood vessel, so that a median as well as two lateral divisions of the coelom, is formed. In the peristomium the dorsal part of these two strands joins with the median walls of the coelomic pouches extending beneath the dorsal longitudinal muscles.

Communication of the coelom with the exterior is maintained by the single opening of the thoracic nephridia, and at the breeding seasons by the gonoducts which are present in most of the abdominal segments.

Feeding

[*The feeding is best studied under a binocular microscope, by examining a worm while still in its tube attached to the stone. This should be so arranged that the observer is looking directly into the branchial crown when spread. There are often small particles in the water to render the currents visible ; if not, a small quantity of carmine mixed with sea water should be put carefully near the crown with a pipette.*]

Since *Pomatoceros* never leaves its tube and since it has no organs other than the branchial crown for food-collecting, its food, which consists of fine plankton and detritus (Hunt, 1925) is restricted to that which can be carried by ciliary currents. Johansson (1927) studied the feeding of *Pomatoceros triqueter* and *Serpula vermicularis ;* the following account agrees in the main with his.

In its normal state of rest, *Pomatoceros* has the branchial filaments of each side spread fairly widely apart, the pinnules extended to meet those of the neighbouring filaments, and that part of the ventral lip which runs round the inside of the branchial lobes is kept apart from them, so that a groove is exposed between. (Text figure 2.)

There are two distinct sets of cilia—current-producing and food-transporting, as in cryptocephalous Polychaetes in general (Orton 1913–15 *a*). The latero-frontal cilia, beating at right angles to the long axis of the pinnules, cause a current of water to be drawn in between the latter. Any food particle brought in on this current becomes entangled in mucus secreted by the glands situated at the sides of the pinnules. It is then taken to the filament by means of the frontal cilia which beat in that direction. The cilia in the filamentar groove beat towards its base and thus the food is carried to the groove between the ventral lip and the filaments. Here the current sets towards the mouth, so that all the food collected by the pinnules reaches the latter. No sorting of food particles takes place, any which are small enough to be carried by the cilia on the pinnules and filaments eventually reaching the mouth.

Johansson found that sometimes food which had passed between the lips was thrown out again on a median forwardly directed current. This he attributed to the presence of taste organs within the lips or oesophagus. The author only found the same occurrence in a worm with the head and two or three segments remaining and never in a whole animal.

If too large masses of food accumulate on the filaments, as may happen when particles are very numerous or too large, the tip of a filament bends over and removes them.

There are three main rejection currents for carrying away food which has collected on some part of the animal other than the grooves of the pinnules or filaments :—

i. A current runs along the inner edge of the palps : most of the material reaching the dorsal surface of the thorax will be taken by the forwardly beating cilia on its surface to one of these.

ii. Another current on the anterior margin of the ventral lip leads outwards on each side to the lateral corners ; particles falling on the ciliated underside of this lip will be carried to the free edge and sent off at its ventral end.

iii. A current drives particles anteriorly along the crests of the basal folds, though the author has only seen this in

> worms removed from their tubes, suggesting that this is masked by other currents when the worm is in its normal position. Soulier (1891) described a similar current in *Serpula* as of great importance in removing particles passed from the ventral lip to the folds, when they came into contact.

The currents of water entering the funnel formed by the branchial crown, due to the beating of the latero-frontal cilia, will cause an outgoing current up the middle of this funnel which takes away any material brought in and not taken up by the pinnules or filaments.

The Alimentary System

ANATOMY.

The alimentary canal is a simple tube ciliated throughout its length without appendages of any kind. It can be divided into five regions, which are not however clearly demarcated from each other.

The mouth (Fig. 18, MTH.) leads into the buccal cavity which is crescent-shaped in section—the concave side being dorsal—and is bounded by the dorsal and ventral lips (Fig. 18, D.L., V.L.). Towards its posterior end the buccal cavity bends ventrally, before passing gradually into the oesophagus. The division between the two is taken for convenience to be the level at which the two halves of the branchial crown join the ventral surface of the ventral lip. The lumen in the anterior part of the oesophagus resembles that of the buccal cavity in shape, but posteriorly it becomes slit-like in section—the greatest diameter usually being horizontal (Fig. 19, OES.)—and finally becomes circular. Its wall appears to be folded and is surrounded externally by a layer of circular muscle (Fig. 19, C.M.) posteriorly, but anteriorly this is only represented by scattered fibres.

At the posterior end of the second segment the oesophagus passes somewhat abruptly into the stomach (Text figure 1, Fig. 18, ST.): this is distinguished from the former by its greater size, by the presence of digestive glands and by a gut sinus (Text figure 1, Fig. 18, G.S.). It is usually oval in transverse section with the greatest diameter dorso-ventrally. The gut sinus extends to the posterior end of the worm and is bounded externally by a thin muscular layer, consisting chiefly of circular muscle fibres (Figs. 21, 22, C.M.).

In the posterior thoracic region the stomach passes into the intestine (Fig. 20, INT.), which is rounder in transverse section and in which no gland cells can be distinguished. It becomes much smaller at the posterior end and its wall becomes more folded. The intestine passes gradually into the rectum, which occupies the last few segments and differs from it only in the possession of mucous cells.

HISTOLOGY.

The epithelium lining the buccal cavity has been described in connection with the branchial crown (p. 15).

The oesophagus is lined by a ciliated epithelium of which the cells vary in height giving the wall a folded appearance ; they are always short in the lateral regions (Fig. 19, OES.). The cytoplasm is somewhat granular, with the elongated nuclei situated towards the base. Mucous glands (Fig. 19, M.G.) are abundant.

The stomach has three kinds of cells forming its epithelium —ciliated cells and two types of gland cells.

The ciliated cells are tall and narrow except at the mid-dorsal and mid-ventral regions where they are much shorter (Text figure 1, ST.). In fixed material the cytoplasm has a somewhat granular appearance with the exception of the distal region where intracellular fibrillae can be seen (Fig. 21). In living cells the distal ends appear colourless, in contrast to the greenish brown colour of the remainder. Oval nuclei (Fig. 21, N.) lie at the base. The basal granules (Fig. 21, B.G.) of the cilia appear to be at the extreme edge of the cell, thus making the basal rods extracellular and the coagulum surrounding the latter a non-cytoplasmic structure as in the mid-gut of *Melinna* (Newell and Baxter, 1936).

The first type of gland cell (Fig. 21, G.C.^{1}) is narrower and appears to be much shorter than the other two ; this, however, is probably because its proximal end is too thin to be distinguished in section. The central part is filled with a substance staining darkly with iron haematoxylin and which can often be seen passing out into the lumen. This type of cell cannot be recognised in sections stained with Azan.

The second type of gland cell (Fig. 21, G.C.[2]) contains darkly staining granules and is usually shorter than the ciliated cells. A darkly staining mass can sometimes be seen extruding from its distal end, apparently formed by the coalescence of numerous granules. In sections stained with Azan similar cells can be seen of which the entire contents may appear yellow, or sometimes the cytoplasm at the proximal end is red and at the distal, yellow. This change in colour is probably correlated with a change in the nature of the secretion between the time of its formation and its liberation into the lumen of the gut.

The intestine is lined by an epithelium consisting entirely of ciliated cells (Fig. 22), which are usually shorter than those of the stomach. The cytoplasm contains numerous small granules staining darkly with iron haematoxylin. Towards the posterior end the cells decrease in height and the cilia (Fig. 22, C.) become longer. The nuclei (Fig. 22, N.), which are oval at the anterior end, here become rounded. The rectum is only distinguished from the intestine by the presence of mucous cells which become very numerous towards the anus, and eventually comprise most of the epithelium.

THE PASSAGE, DIGESTION AND ABSORPTION OF FOOD.

The food entering the buccal cavity is passed along to the oesophagus chiefly by ciliary action, aided by the muscles of the gut wall. Digestion takes place in the stomach, as this is the only region where glands other than mucous cells have been found, and presumably for some distance posterior to it. Passage of food along the stomach and intestine appears to be due mostly to ciliary currents, since the blood passes anteriorly in the gut sinus and the muscles outside the latter must therefore perform chiefly antiperistaltic movements.

In order to find the region of absorption of food animals were fed on iron saccharate and subsequently fixed after varying intervals of time. The middle part of the intestine was found to be the absorbing region. Since specimens fed on insoluble iron saccharate showed numerous blue granules in the ciliated cells, the latter must be able to take in particulate matter, as no amoebocytes have been seen. Similar absorption of solid particles occurs in the liver of many molluscs, such as *Patella* and Tectibranchs, but here the cells, unlike those of *Pomatoceros*, lose their cilia before entering on an absorbing phase.

THE STORAGE OF FOOD.

Fat. This is present in large quantities, especially at the posterior end of the animal. It is found in the connective tissue of the longitudinal muscle of the body, and of the abdominal parapodia and in small amounts in the epithelium of the thoracic body wall. Some is also present in the vacuolated tissue round the oesophagus.

Glycogen. Using Best's carmine method and the iodine method of McClung (1929), the characteristic colour for glycogen may be found in most of the epithelial cells of the anterior body wall and of the branchial filaments. An enormous quantity of glycogen, or, since there is some doubt as to the specificity of Best's carmine stain, some glycogen-like carbohydrate, must be stored in these cells. From Boyland's work on the gills of *Pecten* (quoted by Gray, 1928), it seems that glycogen may be used up during ciliary movement, although he found this substance to make up only a very small percentage of the dry weight of the gill; the storage of glycogen near the ciliated region in *Pomatoceros* may possibly therefore be connected with ciliary activity. On the other hand Yonge (1932) showed that in Crustacea, cuticle is formed from certain epithelial cells in which, at times, Farkas (1927) found that there was much glycogen. It seems probable therefore that in *Pomatoceros*, since most of the anterior end is covered by a thick cuticle, the presence of glycogen or some similar carbohydrate in these cells is concerned with cuticle formation.

The Vascular System

If we accept Lang's theory (1903), which conceives of the vascular system of Annelids as having arisen by the gradual differentiation of definite vessels from an original gut sinus, then the blood system of Serpulids must be regarded as comparatively primitive. From a study of the Oligochaetes Stephenson (1913) concluded that the separation of the ventral vessel in that group began phylogenetically earlier than that of the dorsal and that differentiation has proceeded farther in the anterior than in the posterior region of the vascular system. A comparable process of evolution has apparently taken place in the Serpulids, where there is a definite ventral vessel extending the length of the worm and the anterior end of the gut sinus has become a distinct dorsal vessel, while posteriorly it remains a sinus.

ANATOMY.

The blood system of Serpulids has been studied by several authors, including Claparède (1873), Meyer (1888) and Lee (1912). Its most characteristic feature is the large number of blind-ending contractile vessels. Lee described the vascular system of *Pomatoceros triqueter* as well as other Serpulids and part of the following description is taken from his work.

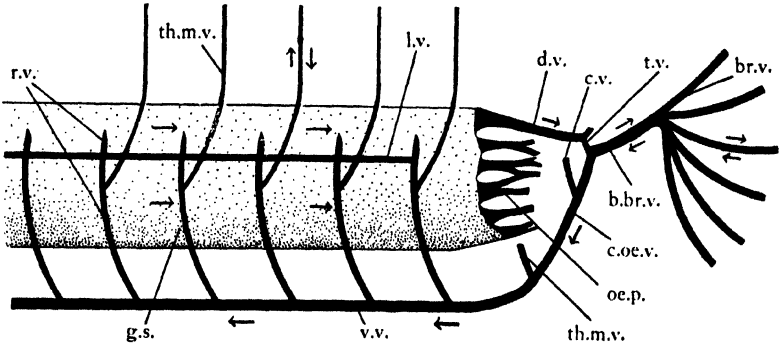
The gut sinus (Text figures 1, 3, Figs. 18, 20, G.S.) surrounds the alimentary canal from the anterior end of the stomach backwards. In front it is continued as a large dorsal vessel and numerous smaller vessels running parallel with it. The smaller of these run within the vacuolated tissue around the oesophagus and the larger are on its surface. Anastomoses occasionally occur between these vessels, forming an oesophageal plexus (Text figure 3, OE.P.).

The dorsal vessel (Text figure 3, Fig. 18, D.V.) which extends to the posterior end of the brain is surrounded by connective tissue. At the anterior end its lumen is almost obliterated in sections owing to the strong sheath of circular muscle surrounding it.

Very short transverse vessels (Text figure 3, T.V.) are formed by the division of the dorsal vessel at its anterior end. Each of these bifurcates to form a basal branchial vessel and a circum-oesophageal vessel.

The basal branchial vessels (Text figure 3, Figs. 5, 19, B.BR.V.) pass between the dorsal and ventral roots of the oesophageal connectives and are continued round the base of each half of the branchial crown, giving off a branchial vessel (Text figure 3, Fig. 8, BR.V.) to each filament. These branchial vessels give off a single blind branch, the pinnule vessel (Fig. 9, P.V.), to each pinnule and themselves end blindly at the distal ends of the filaments. The basal branchial, the branchial and the pinnule vessels all run in coelomic spaces continuous with the coelom of the peristomium.

The opercular vessel is given off from the left basal branchial vessel near the anterior end of the brain and passes up the peduncle.



TEXT-FIG. 3

Pomatoceros triqueter. A diagram of the vascular system, showing the direction of flow of the blood.

b.br.v., basal branchial vessel; *br.v.*, branchial vessel; *c.oe.v.*, circum-oesophageal vessel; *c.v.*, collar vessel; *d.v.*, dorsal vessel; *g.s.*, gut sinus; *l.v.*, lateral vessel; *oe.p.*, oesophageal plexus; *r.v.*, ring vessel; *th.m.v.*, thoracic membrane vessel; *t.v.*, transverse vessel; *v.v.*, ventral vessel.

The circum-oesophageal vessels (Text figure 3, C.OE.V.) pass round the oesophagus and join below to form the ventral vessel (Text figures 1, 3, Figs. 18, 20, V.V.) which extends to the posterior end of the worm, lying in the ventral mesentery. Each circum-oesophageal vessel gives off a collar vessel (Text figure 3, C.V.) to supply the collar, and the first of the thoracic membrane vessels.

Segmentally arranged ring vessels (Text figure 3, R.V.) lying in the coelom, connect the ventral vessel and the gut sinus: the first of these however, according to Lee, runs from the dorsal vessel to the circum-oesophageal vessel, but I have not identified it. The ring vessels are joined by a pair of lateral vessels (Text figure 3, L.V.) extending the length of the worm, probably beginning at the first ring vessel, although their origin has not been traced. The ring vessels are thus divided into dorsal and ventral regions. The ventral parts of those in the thorax, with the exception of the first, and sometimes the first one or two in the abdomen, are much convoluted and covered with chloragogenous tissue composed of small dark cells. This is described later (p. 31). Branches from the ring vessels supply the parapodia and body wall.

Segmentally arranged thoracic membrane vessels (Text figure 3, Fig. 5, TH.M.V.) arise from the lower part of the ring vessels in the thoracic region and run between the two layers of epithelium of the membrane. They give off many branches, which all, after further division, end blindly. The first thoracic membrane vessel comes from the circum-oesophageal vessel as mentioned above.

THE CIRCULATION OF THE BLOOD.

Blood is passed anteriorly along the gut sinus by the contraction of a thin layer of muscle in its outer wall. It thus reaches the dorsal vessel and the oesophageal plexus. From the dorsal vessel the blood passes to the transverse vessels, from which some will go to the basal branchial, branchial and pinnule vessels, and the rest to the circum-oesophageal vessel. Since the branchial and the pinnule vessels end blindly, on their contraction blood passes back from the filaments to the basal branchial vessels and thence to the circum-oesophageal vessels and transverse vessels. Its re-entry into the dorsal vessel is prevented by the circular muscle fibres at the anterior end of the latter, which presumably function as a valve. From the circum-oesophageal vessels it passes into the ventral vessel along which it flows in a posterior direction. The lateral vessels and gut sinus probably receive blood from the ventral vessel by way of the ring vessels as in Sabellids (Fox, 1938 *b*). The thoracic membrane vessels must in this case obtain blood from the ventral vessel, thus ensuring the oxygenation of any which failed to reach the gills or collar. On the contraction of these vessels blood will be returned to the ring vessel and then to the lateral vessel or gut sinus.

THE BLOOD.

The blood is greenish in colour. The pigment is chlorocruorin which is only found in Serpulids, Sabellids and Chlorhaemids; it always occurs dissolved in the plasma and never in corpuscles (Fox, 1926). Chlorocruorin is a substance allied to haemoglobin, but differs from it in its haematin group, which however also contains iron. It has less affinity for oxygen than haemoglobin.

CHLORAGOGENOUS TISSUE.

Clothing the outside of the wall of the ventral part of the ring vessels in the thorax is a mass of dark, small-celled tissue (Fig. 25, CG.T.), usually called chloragogenous tissue. These chloragogenous cells have oval nuclei (Fig. 25, N.) at their distal ends and their cytoplasm stains darkly with iron haemotoxylin; in living material the cells have a brown colour. When fixed and stained for iron, they often give the characteristic blue coloration. Iron is one of the products formed by the breakdown of haemoglobin and Bloch (1939) has shown that in the Glyceridae iron appears when haemoglobin is destroyed. It therefore seems probable that the chloragogenous tissue in Serpulids contains part, at any rate, of the breakdown products of chlorocruorin.

Respiration

Respiratory exchange in the Sabelliformia appears to take place partly through the general surface of the body and partly through the branchial crown. Since all the members of the group are usually tubicolous, the former method necessitates the maintenance of respiratory currents within the tube.

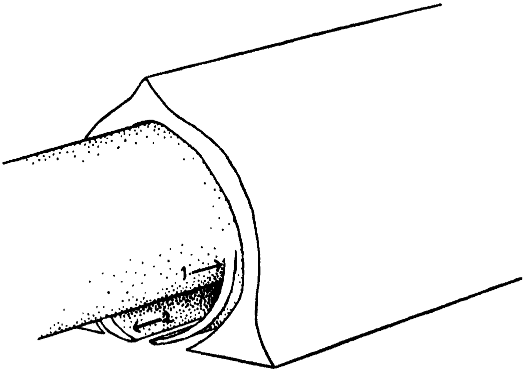
Faulkner (1929) described these currents in *Filograna*, where water enters at the posterior end of the tube and the ventral side of the anterior end, and leaves at the dorsal side of the latter. In *Pomatoceros*, however, where the posterior end of the tube usually becomes blocked, circulation cannot be maintained in this way. The currents are formed chiefly by the cilia on the inner dorsal surface of the thoracic membrane which beat in an antero-posterior direction, and by those on the dorsal body wall and in the groove between this and the thoracic membrane, which beat in the opposite direction. When the membrane is curved over the thorax, which is its natural position when the worm is in its tube, a current which passes backward will be produced at the bottom of the ciliated canal so formed (Text figure 4, arrow 2). The water which is thus caused to enter the tube is returned by the outgoing current on the dorsal surface of the body wall (Text figure 4, arrow 1) and probably does not reach posteriorly beyond the end of the thorax. However, as the thoracic membrane is very thin and is well supplied with blood vessels a considerable part of the respiratory exchange taking place within the tube must occur at its surface, and an efficient circulation of water round the posterior end of the worm is not essential. The frequent contraction and expansion of the abdomen will cause a considerable movement of water round this part of the animal.

On account of its plentiful blood supply, the collar probably also plays some part in respiration (Lee, 1912).

[*The respiratory currents can be seen by removing* Pomatoceros *from its tube and replacing it in a glass one of approximately the same diameter. If a tapering tube is used, the worm can easily be put in at the wide end and, by pushing on the operculum with a needle, be forced down until it reaches a part of suitable diameter. If a little carmine is added or if there are small particles in the water, the two sets of currents on the thorax are apparent if the tube is held sideways and viewed through a binocular microscope.*]

Fox (1933), found that if *Spirographis* is put into a tube of water which is then closed at each end, the circulation of the blood stops after about half an hour, due apparently to the accumulation of carbon dioxide within the tube, and suggested that the same stoppage will normally occur when the worm has been within its tube for some time. Presumably the circulation of *Pomatoceros* will also stop after it has remained within its tube for some time. In those living some distance above low water mark an " oxygen debt " will probably be set up, since the total oxygen content of the blood, both in physical solution and in chemical combination with the chlorocruorin is unlikely to be sufficient to last from the time the circulation stops until they are covered by the tide again.

Stephenson (1913) records a current of water passing a short distance up the alimentary canal from the anus in *Pomatoceros* and other Annelids ; he assumes that the oxygen dissolved in this water can diffuse through the gut epithelium into the gut sinus. This current has not been detected by the author.



TEXT-FIG. 4

Pomatoceros triqueter. A diagram to show the direction of ciliary currents in the thoracic region. The worm is lying in its natural position with its dorsal surface towards the base of the tube and its anterior end to the right of the diagram. The tube and the thoracic membrane have been removed from the left-hand side. For explanation see text.

The Nervous System

[*The nervous system has to be made out from sections because the nerves will not stain with methylene blue and the animal is too small to see them by dissection, except for the ventral nerve cords which are visible in preserved specimens.*]

Quatrefages (1850) gave a brief description of the nervous system of *Pomatoceros* and *Serpula contortuplicata* (= *S. vermicularis*). Later more detailed accounts appeared of that of the Serpulids *Eupomatus lunuliferus* (Meyer, 1888) and *Serpula* *dianthus* (Treadwell, 1891) and again of *S. vermicularis* (Johansson, 1927). These agree in their main features with that of *Pomatoceros.*

The nervous system consists of a brain situated in the prostomium, joined by a pair of short circum-oesophageal connectives to two sub-oesophageal ganglia in the peristomium, and two separate ventral nerve cords passing from these and joined by a transverse commissure in each segment.

The brain (Figs. 18, 19, 26, 27, B) is about 1 mm. wide and 0.25 mm. long. Its double nature is apparent on the ventral surface which is bilobed, and the dorsal groove (Fig. 26, B.GR.), in which the median excretory canal lies, may give further proof of this. Racovitza (1896) divided the Polychaete brain into three parts—anterior, middle and posterior—the first innervating the palps, the second the antennae and the last the nuchal organ. The fore-brain, extended into two lobes supplying the branchial crown, and the mid-brain bearing the oesophageal connectives are both present in *Pomatoceros* but the posterior brain is probably absent, since it appears likely that no nuchal organ is present in Serpulids (Söderström, 1920). The main mass of the brain consists of fibres running transversely (Fig. 19, B.), with a superficial layer of nerve cells, thin ventrally, and not distinct from the connective tissue surrounding the oesophagus.

The circum-oesophageal connectives arise on each side by short thick dorsal and ventral roots (Figs. 19, 27, D.R.C., V.R.C.) enclosing canals through which pass the extensions of the coelom containing the basal branchial vessels. Double roots of this connective are also found in the Sabellidae, Hermellidae and Chlorhaemidae (Johansson, 1927). The dorsal and ventral roots join and almost immediately swell to form the sub-oesophageal ganglia (Fig. 27, S.G.) in the peristomium.

The branchial crown is supplied by two separate pairs of nerves :

i. The internal branchial nerve trunks (Fig. 26, I.BR.T.) arise from a pair of lobes situated somewhat dorsally at the anterior end of the fore-brain. They lie in the connective tissue near the coelomic spaces containing the basal branchial vessels. At the base of the branchial crown each breaks up into a number of nerves, one of which goes to each filament, forming the internal branchial nerve (Figs. 8, 26, I.BR.N.). This lies on the basement membrane of the epithelium at the base of the filamentar groove and gives off a branch into each pinnule. Soon after its separation from the main trunk, the inner branchial nerve of the most dorsal filament on each side gives off a small nerve (Fig. 26) supplying the dorsal (D.L.N.) and ventral (V.L.N.) lips and the palp (P.N.).

ii. The external branchial nerve trunks (Fig. 26, E.BR.T.) arise from the dorsal roots of the oesophageal connectives immediately after these leave the brain and run external to the inner branchial nerve trunks from which they remain distinct. At the base of the branchial crown they break up into several nerves, each of which goes to a space between two branchial filaments, lying on the outside of the coelomic space. Each divides to send a branch, the external branchial nerve (Fig. 26, E.BR.N.) to the filament on either side of it. The nerve going to the first filament divides into two, so that each filament, therefore, has a pair of external branchial nerves, which pass up the outer corners between the bases of the epithelial cells (Fig. 8, E.BR.N.). In *Filograna* (Faulkner, 1929) these give branches to the pinnules, but not in *Pomatoceros*.

This double innervation of the filaments is characteristic of Serpulids (Meyer, 1888; Johansson, 1927).

The opercular nerves (Figs. 19, 26, OP.N.) consist of an external pair formed by the division of a nerve arising from the left side of the brain just posterior to the origin of the left inner branchial nerve trunk, and an internal nerve from the base of the latter. The distribution of the nerves therefore confirms the evidence obtained by a study of development, that the peduncle and operculum represent a modified branchial filament.

The unpaired median dorsal nerve (Figs. 18, 26, M.D.N.) emerges from the posterior end of the brain and runs posteriorly on the ventral surface of the dorsal blood vessel where it appears to end. In *Eupomatus* Meyer thought it continued to supply the gut sinus, but it cannot be traced so far in *Pomatoceros*. The nerve arises by three roots, of which the outer two give off a short branch each side of the median excretory duct.

The oblique branchial nerves (Figs. 26, 27, O.BR.N.) are a pair of stout nerves arising from the dorsal roots of the oesophageal connectives and going to the oblique branchial muscles.

The sub-oesophageal ganglia each give off three main pairs of nerves, in addition to small ones to the ventral body wall :—

i. The lateral sense organ nerves (Figs. 26, 27, L.S.N.), which arise near the junction of the circum-oesophageal commissure with the ganglia, and run to the lateral sense organs.

ii. The collar nerves (Figs. 26, 27, C.N.), which follow the collar blood vessels at first, and although they cannot be seen to enter the collar, probably innervate the latter.

iii. The thoracic membrane nerves (Figs. 26, 27, TH.M.N.), which similarly follow the anterior thoracic membrane blood vessels, and presumably supply the anterior region of the membrane.

Nerves can be seen around the oesophagus in transverse section, but it is not possible to trace their origin. If arrangements in *Pomatoceros* correspond with those in *Eupomatus* (Meyer, 1888) and *Serpula* (Johansson, 1927) they probably arise from the ventral roots of the oesophageal connectives.

The ventral nerve cords are well separated throughout their length, but are farther apart in the thorax than in the abdomen (Text figure 1, Fig. 20, V.N.). They lie immediately within the circular muscle or ventral epithelium. Posterior to each septum, each cord swells to form a ganglion (Fig. 26, G.), those in each segment being connected by a transverse commissure (Fig. 26, T.C.). Nerve cells are practically confined to these ganglia, where they occur on their ventral sides. The segmental nerves (Fig. 26, S.N.) given off from the ventral nerve cord are difficult to follow. Each ganglion gives off two or three which run between the epithelium and the longitudinal muscles of the body wall. Small nerves are also sent to the ventral body wall, presumably corresponding to those of the ventral gland shields of other Serpulids.

The wide separation of the nerve cords in Serpulids appears to be a secondary development rather than a primitive feature, as in young specimens they are nearer together (Hanström, 1928.)

Giant fibres are well developed in *Pomatoceros*, and in the abdominal region may occupy more than half the nerve cord (Fig. 20, G.F.). They begin in the sub-oesophageal ganglia and extend to the posterior end of the worm. Usually only one fibre is visible in each cord, but sometimes there are smaller ones as well which join up at both their ends with the main one. The probable explanation of this is that the giant fibres are compound structures as has been shown to be true for some other Polychaetes (Kappers, 1929). Giant nerve cells are scarce but do occur in the nerve cords.

The great development of giant nerve fibres in Serpulids and Sabellids is probably due to the necessity for rapid contraction of the worms within their tubes at sign of danger. Since only two paths are present the fibres cannot function in the same way as in *Lumbricus* where it has been shown by Stough (1930) that the median fibre transmits impulses travelling posteriorly and the lateral ones those passing anteriorly. As only the anterior end however can receive external stimuli, fibres to conduct impulses anteriorly from the posterior end would be useless.

THE SENSE ORGANS.

Although there are no organs in *Pomatoceros* the function of which is definitely known to be sensory, the dorsal pit and the lateral organs described below appear to have this function.

The dorsal pit (Fig. 18, D.P.) is a backward extension of the ectoderm of the prostomium, to form a short tube dividing posteriorly into blind branches, usually three in number, which sometimes extend a short distance above and below the brain. The pit is lined ventrally with an epithelium resembling that of the outside of the ventral lip, of which it is a continuation, and dorsally with a columnar epithelium covered by a thick cuticle.

This cuticle extends to the dorsal side of the branches. The median branch showed long thin processes, arising from cells which had a more hyaline appearance than the rest of the epithelium.

The paired lateral sense organs (Fig. 28) lie between the sub-oesophageal ganglion and lateral epithelium, and may extend into the collar folds ; they open externally on the ventro-lateral surface of the body by a narrow duct. Each consists of several small cavities bounded by a cubical epithelium. Their function is unknown, but as they are supplied with nerves their function is probably of a sensory nature.

The small sickle-shaped lappets (Fig. 5, L.) previously described, arising between the ventral and lateral collar lobes on each side, may have a sensory function, since a nerve is seen to enter each.

The Excretory System

The excretory organs consist of a large pair of thoracic nephridia, extending through several segments and opening by a median canal on the prostomium. This reduction in the number of nephridia so that the only excretory opening is at the anterior end of the animal is characteristic of Serpulids and Sabellids and has been brought about in relation to their tubicolous habits.

Each nephridium consists of four parts (Fig. 23) :—

i. a ciliated funnel,
ii. a ciliated tube,
iii. an excretory sac,
iv. a median excretory duct leading to the exterior and common to both nephridia.

The ciliated funnels (Fig. 23, C.F.) are fairly small compared with the rest of the nephridia and rather deep ; they lie over the sub-oesophageal ganglia with their openings facing mesially. Each is lined with a cubical epithelium of small ciliated cells.

The narrow ciliated tube (Fig. 23, C.EX.T.) leading from the funnel runs backwards and ventrally to the ventral side of the excretory sac, where it continues posteriorly until it unites with the latter at approximately the segment in front of that in which the sac ends. It becomes considerably expanded for a short distance anterior to the opening. The ciliated tube is often pear-shaped in transverse section due to two or three rows of cells on its median side being taller than the rest. These alone bear the cilia, which are very long, reaching almost to the other side of the tube.

The excretory sac (Fig. 23, EX.S.) is much wider than the ciliated tube and extends through the peristomium and following three or four segments. It lies on the ventral body wall for most of its length, separated from it by connective tissue and in places by muscle (Text figure 1). It is separated from the coelom by the peritoneum. At its anterior end the tube becomes broader and deeper and comes to lie in a lateral position ; there is often an anterior and outward projection towards the base of the branchial crown. A few muscle fibres (Fig. 24, M.F.) are present on its outer surface, and small blood vessels run in the connective tissue bounding it. The cells of its epithelium vary in height ; they may be cubical or three or four times as tall as they are broad, and are often arranged to form fan-shaped groups. Except at their distal ends which are usually free, these cells are always full of small granules (Fig. 24, EX.G.), probably excretory, which stain darkly with iron haematoxylin and yellow with Azan. The distal ends often show small rod-like processes (Fig. 24, R.), not ending on basal granules, and sometimes bear a few long cilia. The nuclei (Fig. 24, N.) are on occasion darkly staining, while those in adjacent cells may stain very lightly, although the cytoplasm has the same appearance in both.

In the second segment each sac gives off dorsally on its median side, a narrow tube, which passes over the dorsal longitudinal muscle and meets its fellow in the mid-line. These narrow tubes are lined with ciliated cells, which however contain granules similar to those in the rest of the excretory sac.

The median duct (Fig. 18, M.EX.D.) is also lined with a flat epithelium, but its cells contain no excretory granules ; it is ciliated at the extreme posterior end only. Where it passes over the brain, this median canal becomes sunk in a groove on its dorsal surface (Fig. 19, EX. D.). Anteriorly it becomes gradually narrower, and opens into the dorsal pit at the anterior end of the latter (Fig. 18, EX.P.).

Meyer (1887, 1888) described the structure and development of the nephridia of the Serpulid *Psygmobranchus* and showed that the funnels and ciliated tubes were derived from the septum behind the peristomium, the excretory sac from a pair of cells which appeared early in development, and the median duct from the dorso-median ectoderm of the body. The nephridia in Serpulids are therefore nephromixia (Goodrich, 1900). In *Psygmobranchus* the nephridia are confined to one segment, therefore until their development in *Pomatoceros* has been ascertained it cannot be said whether its nephridia represent fused pairs belonging to several thoracic segments, or whether they are those of the second segment only which have extended backwards. But as the latter must be true for *Sabella* (see p. 58), this alternative is the more likely for *Pomatoceros* also, although fusion of the nephridia of neighbouring segments has been recorded for some species of Terebellid. (Cunningham, 1888, Hessle, 1917).

[*The dark excretory sac can often be seen through the body wall of a living worm : it can also be made out from preserved specimens which have been bisected longitudinally and from which the gut has then been removed. Details of the nephridia can only be made out from sections.*]

EXCRETION.

When stained by the ammoniacal silver nitrate method for purines (Lison, 1935) the epithelium of the excretory sac and of the narrow limb leading from its anterior end both show purines in some parts, whilst the cells of the median excretory duct never show any. Negative results were obtained using the xanthydrol test for urea.

Waste material is apparently taken up by the cells of the excretory tube directly from the coelomic fluid, since the blood supply to the nephridia is only small. The passage of coelomic fluid along the excretory sac must be due chiefly to the cilia on the funnel and in the narrow ciliated tube, and to the contraction of the muscles running on the outside of the excretory sac, since the cilia in the latter seem to be too sparsely distributed to create an appreciable current. When the excretory materials are in the nephridial cells they are eliminated, on occasions at least, by the liberation of entire cells into the lumen of the tube, since excretory cells complete with nuclei have been found in the latter and in the median canal. Parts of cells or soluble substances may also be excreted. Solid excretory particles from the coelomic fluid will probably be swept directly to the exterior, but the very small lumen of the ciliated tube will prevent any but the finest particles from passing down it.

The Reproductive System

The sexes are separate as in the majority of Polychaetes : they can be distinguished externally at maturity by the difference in colour of the abdomen due to the sex products within, the male being cream and the female a bright pink or orange. At Port Erin, breeding is only recorded in April (Moore, 1937), but worms with ripe ova and sperms have been found at most times of the year at Plymouth (M.B.A., 1931).

It was formerly thought that in Annelids the genital cells were formed from the coelomic epithelium, but Malaquin (1924, 1925) has shown that in the Serpulid *Salmacina* two primitive germ cells can be distinguished in the gastrula stage : these divide and the products of their division form the gonocytes of all segments. These become situated between the coelomic epithelium and the longitudinal muscles but have no connection with the former. It is probable that the germ cells have a similar origin in all Polychaetes, or at any rate in all Serpulids.

The gonads in *Pomatoceros* are situated at the anterior end of each abdominal segment and immediately behind the ring vessel of the segment in front.

The male sex cells are shed from the gonads into the coelom either as spermatogonia or primary spermatocytes—cells with large lightly staining nuclei and very little cytoplasm. In the coelom fairly large dividing cells, probably primary spermatocytes, and other smaller cells with practically nothing visible except a nucleus with well-marked chromosomes, can be seen. The smaller cells are secondary spermatocytes dividing to form spermatids. The spermatozoa have oval heads and long tails.

The female germ cells appear to be liberated at the primary oocyte stage. The ova (Fig. 20, O.) when shed have a definite membrane and a large nucleus with a distinct nucleolus.

The gonoducts, of which there are a pair in each abdominal segment except a few at the posterior end, appear to have a double origin in Serpulids (Meyer, 1887) and are therefore nephromixia like the thoracic excretory organs. They have completely lost their excretory function. Each consists of a ciliated funnel and tube. The funnel is large and lies ventrally at the posterior end of each segment, immediately in front of that in which its duct is situated. The ciliated tube (Fig. 20, OD.) leading from the funnel opens to the exterior on the ventral surface of the worm near the ventral groove (Fig. 20, O.OD.), with the result that the sex cells will be carried along the latter to the anterior opening of the tube. It is lined by a ciliated epithelium, the cilia being long and numerous on the dorsal side, but more sparsely distributed ventrally. Circular muscles near the external openings of the ducts act as sphincters.

[*If a worm containing ripe eggs or sperms is removed from its tube, some sex cells are shed immediately. The passage of eggs along the gonoduct is easily seen on account of the thinness of the ventral body wall; they are passed down in a single row—although this may be two or three cells deep—and ejected singly.*]

The Development

Several authors have described the development of Serpulids, including Soulier (1907) working on *Serpula*, Shearer (1911) on *Eupomatus*, and more recently Segrove (in press with Quart. J. micr. Sci.) on *Pomatoceros*. The following is taken almost entirely from the work of Segrove, who has kindly permitted me to use it before publication.

Cleavage is of the spiral type characteristic of Annelids, and results in the formation of a blastula. Gastrulation by invagination leads to the development of a trochosphere (Fig. 29). This has a well-developed prototroch (Fig. 29, PT.) in front of the mouth, a smaller metatroch (Fig. 29, MT.) behind, and a ventral neurotroch (Fig. 29, NT.) ; there is also a tuft of cilia at each end, the one at the anterior end having an apical organ (Fig. 29, A.O.) immediately beneath it. Feeding cilia (Fig. 29, FE.C.) between the prototroch and metatroch carry food to the mouth (Fig. 29, MTH.) which is ventral. The mouth leads into an alimentary canal in which an oesophagus, a wider stomach (Fig. 29, ST.) and a narrower intestine (Fig. 29, INT.) can be distinguished. The latter opens by the anus (Fig. 29, A.) which is situated dorsally near the posterior end of the larva. A head vesicle (Fig. 29, H.V.), an anal vesicle (Fig. 29, A.V.), one eyespot (Fig. 29, EY.), (the left develops later) and a pair of protonephridia (Fig. 29, PRN.) can also be seen, as well as the beginnings of mesoderm (Fig. 29, ME.).

The larva feeds throughout its pelagic existence, which usually lasts at least three weeks. Metamorphosis occurs when the rudiments of four setigerous segments are present. At this time feeding stops and the region in front of the prototroch and the dorsal and lateral parts of the latter are absorbed. This exposes the lateral folds of the collar, which are formed from the walls of paired invaginations immediately behind the prototroch. Uncini are never present in the first setigerous segment ; in the second and third they appear after the bristles, while in the rest of the thoracic segments they appear before them. This is of interest since Malaquin (1919) found that in *Filograna* those thoracic segments behind the first three setigerous ones are formed by transformation of abdominal ones, and it would thus seem that the three anterior segments differ in some way from the remainder.

Orton (1913-15*b*) found that sexual maturity could be obtained in four months.

[*To carry out artificial fertilisation remove several mature males and females from their tubes and place in clean sea water in a sterilised finger-bowl. Leave for some time until the eggs and sperm have been shed, then remove the worms, decant water and refill with clean sea water. Mix the eggs and sperm with a sterile glass rod and leave the bowl covered. Later change the water.*]

Parasites

The ciliate *Trichodina pediculus* is often observed in fair numbers moving over the branchial crown of *Pomatoceros*, as was first described by St. Joseph (1894). This however is a commensal, not a parasite. There are two or three endoparasitic protozoa which may occur. Gregarines are often present in the gut. In the intestine of one worm St. Joseph found ciliated protozoa, 0·09 mm. long and 0·03 mm. broad, with no mouth and covered with long cilia, which he considered might belong to the genus *Anoplophrya*. I have found one specimen which agrees with this description. Parasites which have the appearance of sporozoan cysts have been found in the anterior region of several worms, usually near the nephridia.

SABELLA PAVONINA.

External Appearance

Sabella pavonina resembles *Pomatoceros* in general appearance. A typical adult worm is 15-20 cm. long and consists of 200-250 segments; it is usually brownish yellow in colour.

The prostomium bears a branchial crown similar to that of *Pomatoceros*, but the basal folds are much better developed. No operculum is present in this or any other Sabellid. There is a median dorsal lip (Fig. 31, D.L.) and one lateral lip (Fig. 31, L.L.) on each side; the two latter enlarge to form a pair of ventral sacs (Fig. 31, V.S.) immediately anterior to their fusion in the median line below the mouth. The palps (Fig. 31, PP.) are relatively much longer than in *Pomatoceros*, being nearly half as long as the filaments. At the base of the branchial crown the dorsal pit opens into the dorsal groove, a median longitudinal ciliated depression on the thorax. Immediately posterior to the external opening of the dorsal pit, the median excretory canal opens into it.

The thorax usually consists of eight segments (Fig. 30), but the number varies in different individuals from six to twelve. The peristomium bears the collar, which is divided into four folds, two dorsal (Fig. 30, D.C.F.) and two ventral (Fig. 30, V.C.F.), which are relatively smaller than in *Pomatoceros*. The ventral sacs are continued backwards between the ventral collar lobes as a pair of parallel folds (Fig. 31, P.F.). Patches of brown pigment occur on the collar and on the base of the branchial crown. The thoracic membrane is absent as in all Sabellidae : this generally provides one of the easiest means of distinguishing them from the Serpulidae, although it is lacking in one or two of the latter, e.g., *Josephella*. The peristomium bears a pair of notopodia similar to those on the other thoracic segments but lacks neuropodia. The notopodia bear long chaetae arranged in two transverse rows, those of the ventral row being shorter. The neuropodia each bear a single vertical row of uncini. The whole dorsal surface is ciliated and bears in addition a median ciliated groove (Fig. 38, D.GR.) taking the place of the two ciliated tracts between the thoracic membrane and the body wall in *Pomatoceros*. In fixed specimens the groove can only be distinguished at the anterior end, where it becomes deeper. The inter-segmental grooves are ciliated, the cilia beating towards the dorsal surface.

The abdomen contains a varying number of segments which become smaller towards the posterior end of the worm. The position of the chaetae is reversed as in all Sabelliformia ; the long ones are arranged in a circle or spiral on short neuropodia and the uncini lie in a single slightly curved vertical row on narrow notopodia (Fig. 30). There is a median ventral ciliated groove (Fig. 30, V.C.G.) which curves up the left side of the body, usually between segments 9 and 10, to meet the dorsal thoracic groove. The rest of the surface is unciliated, with the exception of faint intersegmental grooves on which the cilia beat ventrally. The genital openings, of which there is one pair per segment, are hidden by the neuropodia.

Patches of pigment similar to those occurring on the branchial crown and collar are found behind the uncini in thorax and abdomen. Small pigment spots occur between the notopodia and neuropodia, but often disappear in old individuals.

Ventral gland shields (Fig. 30, V.SH.) are well developed, being absent only from the peristomium. In the thorax they are usually continuous from side to side, but except for the first, they may be divided into two ; in the abdomen they are broken by the ventral groove. They contain numerous mucous glands, which have sunk into the underlying connective tissue from the ventral epithelium. Mucous glands are also present in the parapodia. These all participate in the secretion of the lining of the tube.

The Skeleton and Branchial Crown

In *Sabella* the branchial crown is supported by a skeleton, on to which the muscles working it are inserted. It has been described by Viallanes (1895) and later by Nicol (1930). The skeleton (Figs. 32, 38, SK.AX., SK.SX.) consists of two lamellae lying laterally just beneath the epithelium in the prostomium and peristomium, and joined by a transverse bar above the brain. Near each side of the transverse bar it is pierced by two canals, through which the basal branchial blood vessels pass. Anteriorly it bears supporting rods for the filaments and palps (Fig. 32, SK.P.). The posterior ends of the lamellae lie more dorsally and are used for the attachment of the longitudinal muscles of the body.

The skeletal tissue does not resemble cartilage either histologically or chemically according to Nicol: it consists of two parts, a central axis (Fig. 38, SK.AX.) of large cells filled with fluid and an outer sheath (Fig. 38, SK.S.) of a hyaline substance with the same staining reactions as the basement membrane of the filaments. This sheath contains anastomosing cells.

In each filament is an axis of four rows of cells, surrounded by the sheathing substance (Fig. 37). The pinnules contain only a single row of such cells, of which the ninth forms a bending joint (Nicol, 1930), while the sheath is absent. Apart from the presence of a skeleton, the filaments of *Sabella* differ from those of *Pomatoceros* in the greater development of the basal folds, the presence of only two muscle bands and only two nerves. The ciliated epithelium on the inner sides of the basal folds varies in height; in transverse section the tallest cells are seen at the free edges, which turn outwards, and at the centre of the folds where they form ridges, almost dividing the groove between them into two (Fig. 37). The outer epithelium of the folds is composed of shorter cells, some of which bear cilia. There are numerous mucous glands (Fig. 37, M.G.), particularly towards the free edges.

The pinnules of *Sabella* have one more set of cilia than those of *Pomatoceros*—the abfrontals present on their outer faces. Nicol found these on all Sabellids she examined, but on no Serpulids. In *Sabella* they are borne on two or three rows of cells, and are longer than the frontals. The muscles are in two longitudinal sets instead of one as in *Pomatoceros*, one series lying beneath the epithelium, and another arising from the skeleton of the filament and inserted just above the bending-joint of the pinnule.

The palps have a deep groove bounded by well developed folds. The latter, which contain numerous mucous glands, consist of two layers of epithelium separated by a basement membrane; the outer bears tufts of cilia, while the whole of the inner is ciliated.

[*The skeleton of* Sabella *can be prepared by soaking the anterior end in isotonic* (0·4 M) *magnesium chloride solution for* 24 *hours and then removing the epidermis and muscles with the aid of needles and a brush* (*Nicol*, 1930).]

The Tube

Nicol (1930) gives a detailed account of the building of the tube and also a résumé of earlier work on the subject. The following is based on her work.

Tube formation can take place only when there is a sufficient supply of suitable medium-sized particles from among those collected by the filaments. They are carried to the ventral sacs and there coated with mucus. When the worm is beginning to build, the ventral collar folds are pushed out over the edge of the tube and mud from the ventral sacs is passed to them between the parallel folds, by ciliary currents. These folds supply further mucus. As the mud passes between the ventral collar folds still more mucus is added and the string of mucus-entangled particles is joined to the tube by being pressed between the ventral folds and the body wall. The new piece is drawn out by the rotation of the worm within the tube.

The inner lining of the tube is formed from mucus secreted by the ventral gland shields and the mucous cells of the body wall, and is comparable to the mucoid part of the tube of *Pomatoceros*. The calcareous part of the latter cannot be homologised with the outer part of a *Sabella* tube, since this is not secreted to any great extent by the collar, but consists largely of mud.

If *Sabella* is removed from its tube it cannot form a new one (Fox, 1938*a*), but it can, according to Nicol, form a new posterior end by the secretion from the body wall of mucus to which sand grains adhere. In this it differs from *Pomatoceros* which can secrete only a calcareous plate to block up a break at the posterior end of its tube.

Fox (1938*a*) states that *Sabella* is negatively thigmotropic and geotropic and positively phototropic, and suggests that its ability to digest part of the wall of its tube (Fox, 1933) allows the necessary bending to take place.

The Chaetae

The thoracic bristles, which are not unlike those of *Pomatoceros*, are of two kinds, the dorsal row in each segment containing longer chaetae with longer and narrower wings (Fig. 35) than the ventral. In the peristomium the two rows are not clearly defined.

The abdominal bristles (Fig. 36) are usually all alike : they are somewhat similar to those in the thorax, but have a double curve. In the last 40-50 segments one or more longer chaetae occur in each group, finer than the others and with only one curve. Towards the posterior end the number of bristles decreases and they are not arranged in such definite circles.

The uncini (Fig. 33) are very different from those of *Pomatoceros*; they each have a single main fang with minute teeth on its outer edge (not shown in the figure), and a base much expanded to form a manubrium below the fang. The abdominal uncini are rather smaller and have a shorter manubrium than the thoracic. At the posterior side of each thoracic uncinus is a paddle-shaped bristle (Fig. 34) with a membranous tip, into which the main shaft enters only a short distance. These are absent in the abdomen.

The Muscular System

Since a skeleton is present at the anterior end of *Sabella*, most of the muscles in this region are inserted on it, instead of ending beneath the thickened epithelium of the body wall, as in *Pomatoceros*.

The dorsal and ventral longitudinal muscles (Text figure 6, Fig. 32, D.L.M., V.L.M.) are about equally developed and remain separate throughout their length. The dorsal pair is inserted on the dorsal side of the posterior processes of the skeleton. The ventral pair comes to lie in a lateral position at the anterior end of the thorax and is attached to the outer surface of the same processes. The circular muscles are similar to those of *Pomatoceros*.

The oblique branchial muscles (Figs. 32, 38, O.BR.M.) run from the ventral corners of the branchial crown to the transverse bar of the skeleton, on which some of the fibres are inserted, while others form an anterior transverse band immediately anterior to it, which is not found in *Pomatoceros*. The fibres attached to the transverse bar cause the contraction of each half of the branchial crown as in *Pomatoceros*, while the transverse band will draw the two halves closer together.

A posterior transverse muscle (Fig. 32, P.T.M.) joins the two posterior projections of the skeleton. This apparently helps to spread the branchial crown as Nicol (1930) suggests, and opposes the anterior transverse band, although Orley (1884) considered it to be concerned in closing it.

The branchial muscles (Figs. 32, 37, BR.M.) are arranged in two longitudinal bands. These increase in size towards the base where some fibres are attached to the skeleton of the filament, while others are inserted on the main part of the skeleton. These longitudinal muscles are concerned with the movement of individual filaments, bringing them together by their contraction.

The longitudinal muscles of the pinnule are of two kinds—a series lying beneath the epithelium and confined to the pinnule, the contraction of which will bring about slight bending of the latter, and another set, arising from the skeleton of the filament and inserted just above the bending-joint of the pinnule. This second set alters the position of the pinnule with respect to the filament.

The muscles moving the bristles are similar to those in *Pomatoceros,* but as the parapodia bearing these chaetae are relatively longer in *Sabella,* the retractor muscles, which are attached near the distal ends of the parapodia, will be more effective.

The oblique abdominal muscles are described in connection with the nervous system (p. 57).

[*The longitudinal muscles, and the retractor muscles of the chaetae, can be seen when the worm is cut open along the mid-dorsal line and the body wall pinned out in a stretched condition. The rest of the muscles must be studied from sections.*]

The Coelom

The coelom, which is spacious, is sub-divided in the same way as that of *Pomatoceros,* but has no pouches formed from the peristomial coelom extending beneath the dorsal longitudinal muscles. The latter, however, sends extensions into the branchial crown (Fig. 37, COE.) as in *Pomatoceros.* The peritoneum round the oesophagus is not modified to form vacuolated tissue.

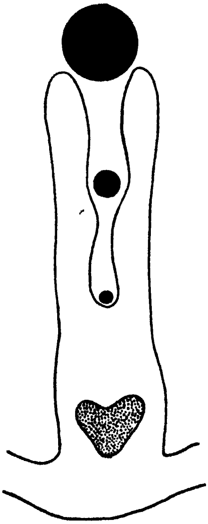
Feeding

[*The feeding may be studied in the same way as for* Pomatoceros (*see p.* 22).]

The food of *Sabella* consists chiefly of bottom-living diatoms, and fine plankton. (Hunt, 1925 ; Nicol, 1930).

The feeding of *Sabella* has been fully described by Nicol (1930), from whose account the following is taken. It differs from that of *Pomatoceros* in the provision of a sorting mechanism, and in a somewhat different method of creating water currents.

Abfrontal cilia, situated on the outer sides of the pinnules, beat from the base to the tip of the latter and the current of water thus created is deflected between the pinnules by the latero-frontals. Particles dragged in by the current are carried by the frontals as far as the distal ends of the basal folds as in *Pomatoceros*. On these sorting occurs (Text figure 5) : particles too large to enter the groove between them are carried on the top of the folds to the dorsal or lateral lips and thence taken to the palps, from the top of which they are thrown off ; medium-sized particles fall on to the ridges on the folds and are carried along the middle of the lips to the ventral sacs for tube-building (Fig. 31, C.G^1.) ; the smallest particles sink to the bottom of the groove between the folds and are carried along the base of the lips to the mouth (Fig. 31, C.G^2.).



TEXT-FIG. 5

Sabella pavonina. A diagrammatic section through a pair of basal folds to show the relative sizes of particles passing along the three longitudinal tracts. (Modified after Nicol.)

The Alimentary System

The alimentary canal of *Sabella* has been described by Nicol (1930). It is divided into the same regions as is that of *Pomatoceros ;* the limits of each region are, as in the latter, ill-defined.

The mouth (Fig. 31, MTH.) leads to the buccal cavity which is lined with a ciliated epithelium in which are numerous mucous cells.

The oesophagus is taken to begin at the fusion of the lateral lips in the mid-ventral line, although there is no sharp demarcation between it and the buccal cavity. Its shape changes gradually so that in transverse section the long axis, which anteriorly is horizontal becomes vertical in the posterior region (Fig. 38, OES.). Its histology resembles that of *Pomatoceros.*

Near the posterior end of the third segment the oesophagus widens to form the stomach, which, like the remainder of the alimentary canal, is surrounded by a gut sinus. The epithelium of the stomach consists of cells which can exist in two physiological states—ciliated and secreting (Nicol, 1930); most of the cells in any given region are in the same state. In this *Sabella* differs from *Pomatoceros*, where glandular and ciliated cells appear to retain their own functions permanently.

The intestine is characterised by the presence of two ventral folds bounding a ventral groove. These folds, however, appear while the secretory epithelium is still present, so there is no sharp distinction between stomach and intestine. The cells forming the folds are tall and bear long cilia; the rest of the epithelium consists of almost cubical cells with shorter cilia.

The intestine merges gradually into the rectum which is lined with an epithelium of tall ciliated cells and contains numerous mucous glands.

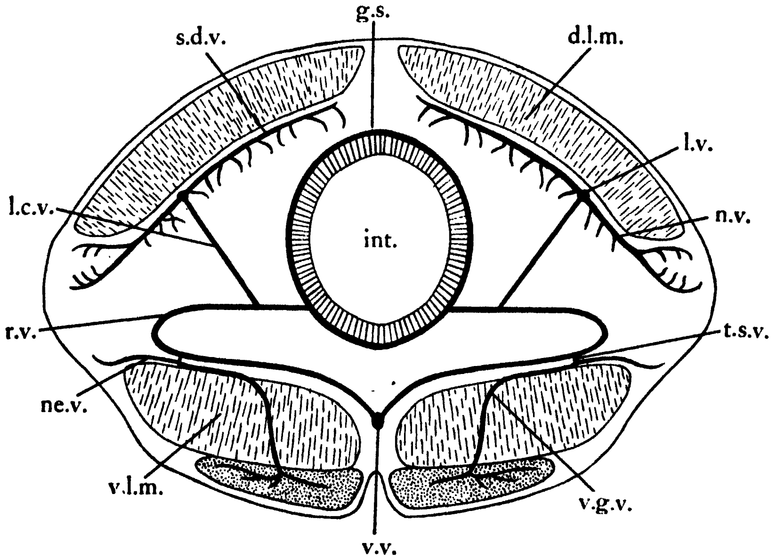
Nicol proved that an amylase, a protease, and a lipase were present in the gut. Her experiments to find the region of secretion, although not conclusive, showed that the anterior end was probably the secretory part.

[*The alimentary canal can be seen when the worm is opened* (*p.* 50), *but the distinction between the stomach, intestine and rectum can only be made out from sections.*]

The Vascular System

The blood system of Sabellids like that of Serpulids is remarkable for its blind contractile vessels. The anatomy of the vascular system of *Sabella pavonina* has recently been described in detail by Ewer (1940), from whose work most of the following is taken. On account of the larger size of the worm details are more easily made out than in *Pomatoceros:* it differs from that of the latter mainly in the following points :—

1. The dorsal vessel arises from the gut sinus by two latero-dorsal vessels.
2. The oesophageal plexus is joined to the circum-oesophageal vessels by a single vessel on each side.
3. The ring vessels (Text figure 6, R.V.), which are only found complete as far forward as the third segment, have a single S-shaped bend near their junction with the ventral vessel (Text figure 6, V.V.).
4. The chloragogenous tissue is present on the ventral vessel as well as the ring vessels but is confined to the S-shaped bend of the latter. It occurs in the abdominal as well as the thoracic segments.



TEXT-FIG. 6

Sabella pavonina. A diagram to show the arrangement of the blood vessels in the abdominal region. (Modified after Ewer.)

d.l.m., dorsal longitudinal muscle; *g.s.*, gut sinus; *int.*, intestine; *l.c.v.*, lateral connective vessel; *l.v.*, lateral vessel; *ne.v.*, neuropodial vessel; *n.v.*, notopodial vessel; *r.v.*, ring vessel; *s.d.v.*, segmental dorsal vessel; *t.s.v.*, trans-septal vessel; *v.g.v.*, ventral gland shield vessel; *v.l.m.*, ventral longitudinal muscle; *v.v.*, ventral vessel.

5. The lateral vessels (Text figure 6, L.V.) are joined to the ring vessels by lateral connective vessels (Text figure 6, L.C.V.).
6. Segmental dorsal vessels (Text figure 6, S.D.V.) arise from the lateral vessels in each segment up to and including the third. These probably correspond to the vessels supplying the body wall arising from the ring vessel in *Pomatoceros.*
7. The notopodial vessels (Text figure 6, N.V.) arise from the lateral vessel instead of from the ring vessels.
8. The lower part of each ring vessel gives off a trans-septal vessel, passing through the septum to the segment behind, where it branches to supply the neuropodium and ventral gland shield. The gland shields of the peristomium and second segment are supplied from the vessels in the ventral collar fold, which arise from the circum-oesophageal vessels.
9. Blind-ending capillaries projecting into the coelom arise from many of the vessels.

The circulation of the blood in Sabellids has been described by Fox (1938*b*) and Ewer (1940). In the main the direction of flow is the same as in *Pomatoceros.* There is no marked development of circular muscle fibres around the dorsal vessel to act as a valve as in *Pomatoceros.* It has been found however, by the above-mentioned authors, that the rate of contraction of the circum-oesophageal vessels is higher than that of the branchial vessels ; this ensures that a considerable amount of the blood from the filaments entering the circum-oesophageal vessels will be taken away by the latter and not remain to be sucked back again into the branchial vessels.

[*The main vessels can be seen when the worm is dissected as for the muscular system ; thick transverse sections of preserved specimens are also useful. Thin sections are necessary to make out the vessels at the anterior end.*]

CHLORAGOGENOUS TISSUE.

The chloragogenous tissue, as in *Pomatoceros*, gives the blue coloration characteristic of iron when stained with potassium ferrocyanide and therefore also possibly contains breakdown products of chlorocruorin. In some specimens large brown bodies were found lying in the coelom: these contained dark granules similar to those of the chloragogenous tissue and when stained, were found to contain iron. Some iron was also found in colourless cells—probably amoebocytes—in the brown masses. It seems probable that the latter are formed by the ingestion of small pieces of detached chloragogenous tissue by amoebocytes, which join together and form an excretory mass. This presumably remains in the coelom throughout the life of the worm. A similar process of ingestion of disintegrated chloragogenous cells by coelomic corpuscles has been described by Cameron (1932) in the earthworm.

Respiration

Respiratory exchange in *Sabella* as in *Pomatoceros* takes place through the branchial crown and general body surfaces. Zoond (1931) working on *Bispira* and Fox (1938*b*) on *Spirographis* found that the oxygen consumption fell to about 37 per cent. of its former value when the branchial crown was removed. It is certain then that in the closely related *Sabella* the branchial crown must also be the chief respiratory organ.

Circulation of water within the tube is maintained entirely by muscular movements of the body and is not helped by ciliary action. A rhythmical pumping action (Nicol, 1930) is caused by the movement of a "piston", formed by the shortening and thickening of a few segments at the anterior end of the abdomen. As it passes backward water is drawn in at the anterior end of the tube in the dorsal and ventral regions where the collar folds do not entirely block the opening. Water is sent out of the tube as the worm returns to its normal length.

The Nervous System and Sense Organs

Pruvot (1885) described the nervous system of *Sabella pavonina* and Meyer (1888) described that of *Spirographis spallanzanii.*

Johansson (1927) re-examined the brain of *Sabella* and found that it agreed in most respects with Meyer's description for that of *Spirographis*.

The following are the chief features distinguishing the nervous system of *Sabella* from that of *Pomatoceros*:—

1. The brain is relatively wider from side to side and shorter in an antero-posterior direction.
2. There is only one pair of branchial nerve trunks, although each arises by two roots. From the position of its branches in the filaments (Fig. 37, BR.N.) this pair would appear to correspond to the internal branchial trunks of *Pomatoceros*. It is probable, however, that each consists of fused internal and external branchial trunks, arising separately from the brain and represented by the two roots. Such a fusion occurs in *Serpula* (Johansson, 1927), but in this case they soon separate again.
3. A pair of nerves (Fig. 38, A.N.) arises from the anterior surface of the brain and passes each side of the median excretory duct. Since a similar pair occurs in *Eupomatus* (Meyer, 1888) it cannot be taken as representing a difference between the Sabellidae and Serpulidae.
4. The median dorsal nerve is only represented by its two roots which join but are not continued posteriorly.
5. The dorsal roots of the oesophageal connectives are much reduced.
6. The ventral nerve cords (Fig. 39, V.N.) lie as close together in the thorax as in the abdomen, unlike those of *Pomatoceros*. Each has an anterior and posterior pair of ganglia (Fig. 39, A.G., P.G.) in every segment, lying near the septa. From both these ganglia arise a dorsal and ventral pair of segmental nerves (Fig. 39, S.N.), the dorsal passing above the ventral longitudinal muscle and the ventral below it. The anterior and posterior ganglia

of each segment are connected by anterior and posterior transverse commissures (Fig. 39, A.C., P.C.); the three most anterior commissures, that is the anterior and posterior of the peristomium and the anterior of the second segment, lie close together. The presence of two pairs of ganglia per segment is not a general distinction between Sabellids and Serpulids as two are present in *Psygmobranchus* (Meyer, 1888).

7. The giant fibres are continued into the oesophageal connectives and in the thoracic region are connected by a collateral in each commissure: such connections cannot be seen in *Pomatoceros*.

In the abdomen a pair of oblique abdominal muscles lies between the posterior commissure of one segment and the anterior commissure of the next, running from above the ventral longitudinal muscle on one side to the median ventral side of the nerve cord on the other.

[*The ventral nerve cords, commissures and segmental nerves can be seen by removing the alimentary canal and nephridia and pinning out the body wall of a few segments in a stretched condition. The brain and the nerves arising from it can only be studied from sections.*]

The dorsal pit (Fig. 38, D.P.) divides into three processes, of which the two lateral ones go farther back than in *Pomatoceros*, extending some distance along the outer sides of the brain. The posterior ends of these lateral processes have the appearance of simple eyes, with pigment cells and a central core of cuticle (Nicol, 1930). They have been shown to be formed by the covering over of larval eyes in *Branchiomma* (Wilson, 1936) and from their position can obviously have no visual function in the adult.

The Excretory System

The excretory organs in *Sabella* consist of a single pair of nephridia opening anteriorly by a median duct as in *Pomatoceros*, but extending further back and lying freely in the coelom, kept in position only by septa. Since gonoducts are found in some of the same segments as the nephridia, it appears that in *Sabella* the latter are formed from a posterior extension of a single pair of nephridia.

Each ciliated funnel opens into the peristomium and leads into a light coloured tube which is much wider than the narrow ciliated tube of *Pomatoceros* and bears true cilia at its anterior end only. In other parts its cells resemble those of the wider tube into which it opens in one of the posterior thoracic segments. The wider tube extends into the first or second abdominal segment and then runs anteriorly as far as the peristomium, lying on the median side of the narrower tube. There it narrows and passes dorsally inside the circular muscle of the body wall to join its fellow in the middle line. The median duct (Fig. 38, M.EX.D.) thus formed opens into the anterior end of the dorsal pit, some distance in front of the brain. Until the development of the nephridia of the two species has been described it is not possible to decide whether the whole of the narrow tube corresponds to the ciliated canal of *Pomatoceros*, and the wider tube to the excretory sac, or whether the latter is represented also by the unciliated part of the narrow tube.

From the resemblance of the epithelium of the wider tube and the posterior part of the narrower tube to that of the excretory sac of *Pomatoceros*, it appears probable that excretion is carried out by both parts.

[*The excretory sacs and funnels can be made out after removing the alimentary canal; to see the narrower lighter tube remove a sac and turn it over. The fusion of the two wider limbs to form a median duct can best be seen in transverse sections through the anterior thoracic region.*]

The Reproductive System and Development

The sexes are separate but there is no marked difference in colour between mature males and females as in *Pomatoceros*, since the thicker body wall masks the colour of the sex products. Worms with ripe sex products occur at Plymouth during August and September (M.B.A., 1931).

The gonads are situated in the abdomen. The genital ducts are very short and open beneath the neuropodia, therefore the intersegmental ciliated tracts on the ventral surface of the abdomen probably carry sex products from the genital openings to the ventral groove, on which they will be taken to the anterior opening of the tube.

Wilson (1936) described the development of *Branchiomma vesiculosum*, as he found it impossible to obtain successful fertilisations of *Sabella*. By comparison with a few early stages of the latter obtained by Orton, however, he found the two larvae were very similar. The larva of *Branchiomma* has a broad prototroch and a ventral neurotroch as in *Pomatoceros*, but no teletroch. After about 24 hours it begins to elongate and segment ; two anal vesicles and a head vesicle can be seen, similar to those in *Pomatoceros* although in the latter the anal vesicle is unpaired. The mouth opening is visible on the third day but the larva does not feed until just before or during metamorphosis, owing to the large amount of yolk present in its tissues ; in this it differs markedly from *Pomatoceros*. Fixation takes place at eight or nine days and the larva, usually with three or four segments, attaches itself by a tube of mucus. Metamorphosis begins and most of the tissue anterior to and including the prototroch breaks down to form an anterior protuberance which later becomes broken off in small pieces, not absorbed as in *Pomatoceros ;* the remaining part of the head becomes joined to the trunk. The thoracic segments have dorsal bristles and ventral uncini from the beginning as in *Pomatoceros ;* the remaining ones are of the abdominal type. In the regeneration, however, of a worm which has been cut through the abdomen, some of the anterior segments of the posterior piece become transformed into thoracic (Berrill, 1931), a change comparable to that occurring during the development of the Serpulid *Filograna* (Malaquin, 1919).

[*To make an artificial fertilisation of* Branchiomma (*Wilson,* 1936)—*wash out the contents of the body cavity of* 30–40 *mature males and females into a bowl containing a little sea water, and* *stir thoroughly. After half-an-hour wash away excess sperm by decanting several times with fresh sea water. Distribute the eggs between several finger bowls and as the majority never segment, the next day pipette the swimming larvae to clean bowls. At the end of the free-swimming stage add a few drops of a* Nitzschia *culture.*]

AMPHITRITE JOHNSTONI.

External Appearance

A large specimen of *Amphitrite johnstoni* may be as much as 25 cm. long and up to 2 cm. in diameter at its anterior end. The worm is brown to pink in colour, with cream-coloured tentacles and red gills. The body can be divided into head, thorax and abdomen ; the mouth and anus are terminal.

The head is formed of fused prostomium and peristomium (Fig. 40, PR., PER.). The prostomium is pulled out to form two lateral lobes and bears tentacles (Fig. 40, T.) at its anterior end ; the bases of these are covered by a fold, which probably represents fused antennae (Nilsson, 1912). The tentacles, which are capable of elongation to many times their normal length, carry a pair of folds at their proximal ends. Nilsson considers the tentacles of Terebelliformia correspond to the palps of Errant Polychaetes ; in this case they are homologous with the branchial crown of the Sabelliformia. The anterior part of the peristomium forms the ventral lip (Fig. 40, V.L.), the mouth being situated between this and a large upper lip (Fig. 40, D.L.) arising from just beneath the tentacles. This dorsal lip also belongs to the peristomium (Fauvel, 1927).

The thorax consists of the 26 segments behind the peristomium. The first three of these, that is the 2nd, 3rd and 4th body segments, each bear a pair of branched gills (Fig. 40, GL.). In the living animal they are continuously moving and change from bright red to orange in colour as their blood vessels expand and contract. The gills probably represent cirri (Nilsson, 1912) and are therefore homologous with the anterior part of the thoracic membrane of Serpulids. These same three segments each bear a pair of lateral lobes (Fig. 40, L.LB.) at their anterior margins.

The first three body segments are achaetous, the 4th bears bristles and no uncini, while the 5th and succeeding thoracic segments bear dorsal bristles and ventral uncini. The long chaetae (Fig. 40, TH. BR.) are arranged on short notopodia (Fig. 40, NOT.) and lie vertically instead of horizontally as in *Pomatoceros* and *Sabella*. The neuropodia are long, low, vertical swellings bearing the uncini (Fig. 40, TH. UN.).

External nephridial openings (Fig. 40, EX.P.) occur on all segments from the 3rd to the 15th or 16th. On segments 3, 4 and 5 they are at the tips of small papillae, which lie immediately ventral to the gills in segment 3, and between the notopodia and neuropodia in the other two segments. In segments 6 –15 or 16 the openings may lie on papillae as in the anterior segments, or appear as small pores in the centre of raised cushions lying between the noto- and neuropodia.

A so-called " collar " (not homologous with that of the Sabelliformia) is present on segment 2. Ventral gland shields (Fig. 40, V.SH.) are present on segment 3 and about the following thirteen segments. Anteriorly they are well developed but posteriorly become much smaller. They secrete the mucus which lines the burrow and therefore have the same function as in *Sabella*. The ventral glands (Fig. 49a, V.GL.) supplying them project into the coelom as numerous yellow bodies around the ventral blood vessel.

The abdomen in large specimens consists of from 75–85 segments and shows a greater tapering towards the posterior end than in *Sabella* or *Pomatoceros*. In specimens removed from their tubes it is generally coiled. It is distinguished from the thorax by the absence of bristles. The anus is elongated vertically. There is no ciliated groove such as is present in the Sabelliformia.

In the thorax and anterior region of the abdomen the boundaries of the segments are obscured externally by the presence of numerous transverse striations.

The Chaetae

The position of the long chaetae has already been described. They bear wings as in *Pomatoceros* and *Sabella* but these do not extend to the distal end, which is toothed (Figs. 44, 45). The bristles of the anterior row of each segment are shorter than those of the posterior row and have their toothed portion, which is slightly curved (Fig. 45), set at an angle to the main shaft, instead of being in the same straight line with it.

The uncini, which are similar in thorax and abdomen, are arranged in two rows from one of the anterior chaetigerous segments, to the 1st, 2nd or 3rd abdominal segment inclusive; elsewhere they are in one row. Each uncinus (Fig. 43) bears one large long tooth and several rows of much smaller teeth behind it. The arrangement of these in rows can only be seen when looking at the edge of an uncinus. A projection from the basal part extends towards, or may meet, the large tooth, and two smaller projections from the opposite side each bear a long thin bluntly ending chitinous rod. These thin rods, which are embedded in the body wall, and whose function is to support the uncini, are formed from the cells of the chaetal sac in the same way as the latter (Hessle, 1917). No such supporting structures occur in *Pomatoceros* or *Sabella*. When the uncini are in a single row the teeth point forward: when in a double row the hooks of the uncini of one row alternate with those of the other and the teeth face each other. Those with their teeth facing anteriorly will help in movement backwards along the tube, while those in which they face posteriorly will assist forward locomotion.

The Tentacles

The tentacles of *Amphitrite* are concerned chiefly with feeding and do not create a current of water which will be of use in respiration, as does the branchial crown of the Sabelliformia. The presence of definite gills makes the respiratory function of the tentacles much less important, and with this can be correlated the lack of blood vessels. The absence of pinnules is connected with the different method of food collecting.

The tentacles, which in section have their greatest diameter from side to side (Fig. 41), become much narrowed immediately anterior to their insertion on the prostomium. Each bears on its adoral face a ciliated groove (Fig. 41, C.G.) which stops a few millimetres from the proximal end.

The epithelium bounding the tentacle is unciliated except in the groove ; here the cilia are usually longer at the base instead of at the edges as in *Pomatoceros*. The cells vary in height in fixed material and the boundaries between them are difficult to distinguish. Their granular cytoplasm, which stains fairly darkly with iron haematoxylin, is in marked contrast to that of the empty-looking cells of the filaments in *Pomatoceros*. Mucous cells (Fig. 41, M.G.) occur in and near the groove. Beneath the epithelium is a narrow layer of circular muscle (Fig. 41, C.M.) succeeded by a much thicker layer of longitudinal muscle (Fig. 41, L.M.) which becomes very thin near the groove, with the exception of one large band immediately below. Nerves (Fig. 41, T.N.), usually three in number, run between the circular muscle and the epithelium on the aboral side of the tentacle. The centre contains an extension of the coelom (Fig. 41, COE.) as in *Pomatoceros* and *Sabella*, but no blood vessel. This coelomic cavity contains many coelomic corpuscles and is traversed by muscle fibres (Fig. 41, M.F.), passing from the longitudinal muscle on the outer side of the tentacle to that beneath the groove.

The Gills

Each gill (Fig. 40, GL.) arises from the body by a short thick stem, which soon divides, often dichotomously, to form a number of small branches. These are usually spirally coiled, and keep up a continual writhing movement during life.

In transverse section each gill is seen to be bounded by a columnar epithelium (Fig. 42, EP.), containing some mucous glands. Immediately beneath this is a layer of longitudinal muscle (Fig. 42, L.M.), except at each side where it is separated from the epithelium by a large blood vessel (Fig. 42, B.V.). These two vessels join at their distal ends. The longitudinal muscles project into the coelomic cavity (Fig. 42, COE.) which occupies the rest of the section, and like that of the tentacles, is packed with coelomic corpuscles.

The Muscular System

The body wall has a longitudinal and circular series of muscles. The circular muscles (Fig. 47, C.M.) lying below the epithelium, form a much thicker layer than in the Sabelliformia.

The longitudinal muscles are arranged to form a dorsal and ventral pair (Fig. 47, D.L.M., V.L.M.) in the region of the intestine, but anteriorly the distinction between the dorsal ones becomes lost. They do not form compact bundles as in *Pomatoceros* and *Sabella* but project as many ridges into the coelom. The dorsal muscles extend to the posterior end of the brain ; the ventral ones, which in the anterior thoracic region take up a more lateral position, join anteriorly to form a thick transverse band at the level of the anterior surface of the brain, lying immediately below the base of the tentacles.

Oblique muscles (Fig. 47, OB.M.) are well developed. Laterally they are attached to the body wall ventral to the dorsal longitudinal muscle, and ventrally near the mid-ventral line. From the 5th segment to the posterior end of the worm they form a nearly continuous sheet, but anterior to this they are more interrupted.

A median ventral longitudinal muscle (Fig. 53, M.V.L.M.) overlies the nerve cord throughout its length.

The muscles of the tentacles and of the gills have already been described (p. 63) and the muscles of the alimentary canal are described in a later section (p. 67).

The muscles moving the bristles comprise both extensors and retractors. The extensor muscles resemble those of *Pomatoceros* and *Sabella*, but there is a single retractor muscle attached to the base of each chaetal sac, which passes across the coelom to its insertion on the mid-ventral line of the body wall as in *Arenicola* (Ashworth, 1904). This represents a mechanical improvement on the arrangement of the retractors in *Pomatoceros* and *Sabella*.

Short suspensory muscles (Fig. 47, D.S.M., V.S.M.), passing from the mid-dorsal and mid-ventral lines of the body wall to the alimentary canal hold the latter in position. They are absent only from the anterior thoracic region.

[*Most of the muscles can be seen on opening the worm by a cut slightly to one side of the mid-dorsal line—to avoid cutting the dorsal suspensory muscles—and pinning out the body wall in a stretched condition. The coelom should be washed clean of coelomic corpuscles. The exposure of the median ventral longitudinal muscle should be left until the dissection of the nervous system as it is overlain by the alimentary canal and ventral blood vessel.*]

The Coelom

The coelom of the Terebelliformia differs from that of the Sabelliformia in the absence of septa between most of the anterior segments. Meyer (1887) described the division of the coelom in *Amphitrite rubra* in detail, and it agrees closely with that of *A. johnstoni*.

In *Amphitrite johnstoni* septa are absent from the first 40–50 segments, with the exception of a thick diaphragm (Fig. 49a, D.) near the anterior end dividing the aseptate region into anterior and posterior chambers. It is difficult to determine the exact position of the diaphragm by dissection, but it appears to be inserted between the 4th and 5th segments as in Terebellids in general (Hessle, 1917). Its insertion on the alimentary canal is somewhat posterior to that on the body wall, so that a shallow funnel is formed. This diaphragm has four posteriorly directed sacs (Figure 49a, D.S.). Hessle agrees with Meyer (1887) that by their contraction they help in the extension of the tentacles, driving coelomic fluid into them from the anterior body chamber. In support of this view he mentions the absence of these pouches in the related Amphictenidae and Ampharetidae, where the tentacles are shorter and where, therefore, contraction of the diaphragm alone should suffice to expand them. The waves of contraction which pass forwards over the anterior part of the body are rhythmical and cannot be the cause of the movements of the tentacles which are quite irregular. The rapid motion of coelomic corpuscles up and down the tentacles, quite apart from the extension or contraction of the latter, may be due to slight vibrations of the entire diaphragm. A pair of similar sacs are found on the first diaphragm of *Arenicola*, and it is possible they play some part in extruding the buccal mass (Ashworth, 1904), although Wells (1937) considers a dorsal fold in the diaphragm is probably of importance in this connection.

After the first 40–50 segments, intersegmental septa appear (Fig. 49b, SEP.) and continue to the posterior end of the body. There is apparently no connection between the coelomic cavities of neighbouring segments in this region.

The body cavity is further divided fairly completely into three longitudinal divisions by the oblique muscles (Fig. 47, OB.M.). The dorsal and ventral suspensory muscles (Fig. 47, D.S.M., V.S.M.) supporting the alimentary canal except at its anterior end, take the place of the dorsal and ventral mesenteries of other Polychaetes, and sub-divide the median chamber into right and left halves.

The three kinds of coelomic corpuscles found in Terebellids (Picton, 1898) are all present in *Amphitrite johnstoni* :—

i. eleocytes, which are the largest and most numerous and are responsible for the pink colour of the coelomic fluid. They are approximately spherical and contain large granules, probably of a lipoid nature, and smaller albuminous ones (Fauré-Fremiet, 1929). The pink colour does not appear to be due to haemoglobin, since spectroscopic examination failed to show absorption bands of any haemoglobin derivative.

ii. fusiform bodies containing a mass of dark granules except at their ends, which are clear.

iii. amoebocytes.

[*The best way of examining the sacs on the diaphragm is to cut a thick transverse section of a worm which has been preserved in alcohol. The three kinds of coelomic corpuscles can easily be seen by mounting a drop of fresh coelomic fluid on a slide and examining under the microscope.*]

The Alimentary System

[*The alimentary system is exposed when the worm is opened to show the muscular system* (*see p.* 65).]

ANATOMY.

The regions of the alimentary canal of *Amphitrite* are much more sharply defined than in *Sabella* or *Pomatoceros*.

The mouth leads into a pharynx (Fig. 49a, PH.) expanded from side to side, of which the floor is raised by a mass of loose tissue in the region of the 2nd segment to form a conspicuous swelling. Posteriorly the pharynx becomes much narrower and passes gradually into the oesophagus (Fig. 49a, OES.); the division between the two is taken to be at the diaphragm between the 4th and 5th segments. Numerous blood vessels run on the surface of both. At about the 12th segment the oesophagus opens into the much larger stomach. This can be divided into two regions, an anterior stomach (Fig. 49a, A.ST.), which appears yellow owing to a covering of chloragogenous tissue, extending to the region of the 18th segment, and a posterior stomach (Fig. 49a, P.ST.) which presents a glistening appearance due to the thick layer of muscle surrounding it. In the neighbourhood of the 28th segment the stomach passes into the narrower anterior intestine (Fig. 49b, A.INT.), which is much coiled and often causes the body wall to bulge: this is also covered with yellow tissue. The posterior intestine (Fig. 49b, P.INT.) into which it leads is straight and extends to the anus; it is somewhat constricted by the septa (Fig. 49b, SEP.) which occur between the segments in this region of the body.

HISTOLOGY.

The oesophagus differs from that of *Pomatoceros* in possessing a well marked layer of longitudinal muscle and in the much greater folding of its walls due to differences in height of the epithelial cells.

The anterior stomach has a layer of muscle external to the gut sinus, and is lined by an epithelium of columnar cells bearing a brush border. In addition to mucous glands, other gland cells are present, which stain more darkly than the rest of the epithelium, and which are probably digestive in function.

The posterior stomach has a much thicker layer of muscle (Fig. 48, M.F.); the fibres seem to vary in direction, sometimes appearing as if they are at right angles to the gut wall. The sinus (Fig. 48, G.S.) separating this from the stomach epithelium is traversed by occasional strands of connective tissue. Similar strands crossing the gut sinus have also been described in some of the Sabelliformia (Claparède, 1873; Lee, 1912). The epithelium (Fig. 48, EP.) consists entirely of cells bearing a brush border similar to that of the anterior stomach, but here it is covered with a thick membrane (Fig. 48, MB.), staining a faint blue with Azan, except for a pinkish layer near the brush border. Similar membranes are found in the mid-gut of *Melinna* (Newell & Baxter, 1936), the crop of *Aphrodite* (Fordham, 1925) and the intestine of *Peripatopsis* (Manton, 1937), but they probably differ in chemical composition.

The anterior and posterior intestine are both covered by a layer of muscle, which is separated from the epithelium by a gut sinus (Fig. 47, G.S.). In both regions there are two large ventral folds, much better developed than in *Sabella*, with a deep groove (Fig. 47, V.G.) between. In the anterior intestine only the cells lining the groove, which are shorter than the others, bear true cilia; the remainder end distally in a brush border covered by a thin membrane. The posterior intestine is lined throughout by a ciliated epithelium, the cilia being longer in the ventral groove.

THE PASSAGE AND DIGESTION OF FOOD.

The food taken in at the mouth is passed along the pharynx and oesophagus to the stomach by combined peristalsis and ciliary action. Owing to the presence of numerous mucous glands in these regions the gut epithelium will be protected from any sand grains or other hard particles entering with the food.

Digestion is probably initiated in the anterior stomach, since gland cells other than mucus-secreting ones are present. The posterior stomach appears from its structure to have the function of a gizzard, as its muscular walls would exert a powerful crushing action on the food, and the thick membrane would protect the gut epithelium during the process. Passage of food through the stomach must be effected only by muscular action, since no true cilia are found. This will ensure a more thorough mixing of the enzymes with the food than would be possible if the latter were carried by ciliary currents.

The coiling of the anterior intestine, giving a much greater surface, suggests that this is the chief region of absorption, the posterior end continuing the process. The absence of gland cells in either region supports this view. Passage of food through this region must be brought about largely by ciliary action, since the gut musculature is not well developed. In the anterior intestine its movement must be almost confined to the ventral groove, which is the only part to bear cilia.

The Vascular System

ANATOMY.

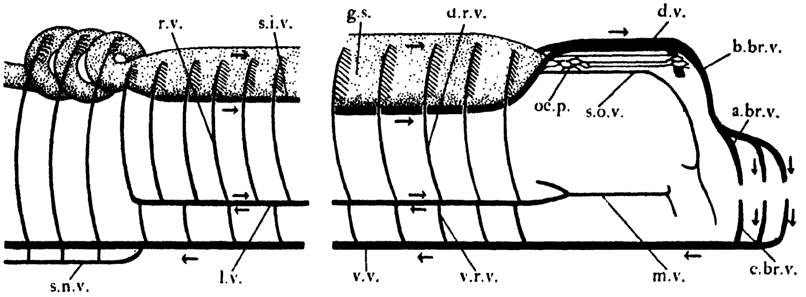
The blood system of *Amphitrite johnstoni* resembles that of *A. rubra* (Meyer, 1887). It differs markedly from that of the Sabelliformia in the absence of blind vessels.

A gut sinus (Text figure 7, Fig. 47, G.S.) surrounds the stomach and intestine. At its anterior end the sinus breaks up into an oesophageal plexus (Text figure 7, OE.P.) over the posterior part of the oesophagus; this plexus then forms several longitudinal vessels, which join anteriorly to form a pharyngeal plexus. Among the longitudinal vessels a sub-oesophageal vessel (Text figure 7, S.O.V.) can be distinguished, which, towards the anterior end of the oesophagus, separates from the latter and passes ventrally, dividing to form two branches.

A pair of sub-intestinal vessels (Text figure 7, Figs. 47, 49a, S.I.V.) lie close together beneath the gut sinus, connected to it by numerous short connecting vessels. At the anterior end of the stomach the two vessels diverge to turn dorsally where they unite to form the dorsal vessel (Text figure 7, Fig. 49a, D.V.), lying above the oesophagus and attached to it by muscles. The dorsal vessel contains a heart body to be described below (p. 71).

The basal branchial vessels (Text figure 7, B.BR.V.) are formed by the bifurcation of the dorsal vessel immediately in front of the diaphragm. These send an afferent branchial vessel (Text figure 7, A.BR.V.) to each gill.

The efferent branchial vessels (Text figure 7, (E.BR.V.) of the first gill unite to form the ventral vessel, and the other two pairs of efferent branchials open into this. The ventral vessel (Text. figure 7, Figs. 47, 49a, V.V.) runs throughout the length of the worm, and in the thoracic region receives small vessels from the ventral glands. A supraneural vessel (Text figure 7, S.N.V.) lies below the ventral vessel in the region of the intestine and posterior stomach. Short branches connect it to the ventral vessel.



Text-Fig. 7

Amphitrite johnstoni. A diagram of the vascular system, showing the direction of flow of the blood.

a.br.v., afferent branchial vessel; *b.br.v.*, basal branchial vessel; *d.r.v.*, dorsal ring vessel; *d.v.*, dorsal vessel; *e.br.v.*, efferent branchial vessel; *g.s.*, gut sinus; *l.v.*, lateral vessel; *m.v.*, median vessel; *oe.p.*, oesophageal plexus; *r.v.*, ring vessel; *s.i.v.*, sub-intestinal vessel; *s.n.v.*, supra-neural vessel; *s.o.v.*, sub-oesophageal vessel; *v.r.v.*, ventral ring vessel; *v.v.*, ventral vessel.

A pair of lateral vessels (Text figure 7, L.V.) are present in the region of the stomach, lying in the coelom and joining anteriorly to form a median vessel (Text figure 7, M.V.). Paired dorsal ring vessels (Text figure 7, Fig. 49a, D.R.V.) connect the gut sinus and lateral vessels; they lie on the outer edge of mesenteries connected to the gut sinus, and give off fine branches to the latter. These dorsal ring vessels are arranged segmentally in the region of the anterior stomach, but in that of the posterior stomach they are more numerous than the segments.

Paired segmental ventral ring vessels (Text figure 7, Fig. 49a, V.R.V.) connect the lateral and ventral vessels.

In the intestinal region where the lateral vessels are absent, the gut sinus and ventral vessels are joined directly by a series of paired ring vessels (Text figure 7, R.V.).

THE HEART BODY.

The heart body (Fig. 50) consists of an irregular spongy mass of cells partially blocking the lumen of the dorsal vessel, and at its posterior end projects into the two branches which pass dorsally from the sub-intestinal vessels. In parts the heart body is traversed by strands of muscle. It is composed of small cells of which the boundaries are indistinct and is bounded by pavement epithelium.

Nothing comparable to a heart body occurs in the Serpulidae or Sabellidae, but similar organs occur in other families of Polychaetes, although it is probable that they are not homologous throughout the group (Fauvel, 1897). Picton (1898) gave a summary of the functions attributed to the heart body by various authors. Bloch (1939) found that in Terebellids it contains iron and appears to be one of the regions in which destruction of haemoglobin occurs. In *A. johnstoni* it probably also prevents a back-flow of blood into the dorsal vessel on contraction of the gills ; if so it is analogous to the circular muscle round the dorsal vessel acting as a valve in *Pomatoceros.*

It can be seen that the blood system of *Amphitrite* is built on the same general plan as that of *Pomatoceros*. The gut sinus, ventral vessel and ring vessels appear homologous ; the sub-intestinal vessels which anteriorly turn dorsally to form the dorsal vessel, have not become separated from the gut sinus in *Pomatoceros*. The branchial vessels cannot be homologised, since the structures which they supply are probably formed from different appendages in the two genera.

THE CIRCULATION OF THE BLOOD.

The circulation of the blood is probably as follows :—The gut sinus and sub-intestinal vessels send blood anteriorly : that in the former goes to the vessels on the oesophagus and thence to the pharynx ; that in the latter enters the dorsal vessel and is carried to the gills by the afferent branchial vessels. After oxygenation it is taken back to the ventral vessels by the efferent branchials, re-entry into the dorsal vessel being prevented by the presence of the heart body. Blood is sent from the ventral vessel to the gut sinus by the ring vessels. In the lateral vessels blood will flow in both directions.

THE BLOOD.

The blood differs in colour from that of *Pomatoceros* and *Sabella*, being reddish instead of greenish. This is because the blood pigment is haemoglobin instead of chlorocruorin. In Terebellids, according to Bloch (1939), haemoglobin is formed in the papillae of the ventral shields and its destruction takes place in the heart body and parts of the digestive tube.

Respiration

The chief organs of respiration in *Amphitrite* are the gills. Bounhiol (1902) found that on their removal in *A. edwardsi* there was a reduction of 75 per cent. in carbon dioxide excretion ; it would appear therefore that they play a more important part in respiration than does the branchial crown of *Sabella*. This may be partly accounted for by the presence of distinct afferent and efferent branchial vessels which allow a continuous exchange of oxygen to take place, whereas if only one vessel is present, it must be emptied of blood on every contraction ; the continual movement of the gills of *Amphitrite* ensures a renewal of the water surrounding them. Bounhiol also showed that the tentacles are of some use in respiration.

The rhythmical waves of contraction of the body wall will ensure renewal of the water within the tube, and some gaseous exchange will take place through the general body surface.

According to Stephenson (1913) intestinal respiration takes place in one species of *Amphitrite*.

Nervous System

The nervous system of the Terebellidae is less differentiated from the epithelium than in the Serpulidae or Sabellidae. The brain in *Amphitrite* is situated in the prostomium, immediately behind the tentacles. It is much simpler than in *Pomatoceros*, consisting merely of a band of nervous tissue lying beneath the dorsal epithelium, with no distinct division between the two. The band is composed of a layer of fibrous tissue overlain dorsally by a layer of large nerve cells. Nilsson (1912) homologises the tentacles of the Terebelliformia with the palps of Errant Polychaetes because of their innervation from the posterior border of the anterior brain, but the three divisions of the brain (Racovitza, 1896) cannot be distinguished in *Amphitrite*. The brain passes gradually into the oesophageal connectives which run beneath the epithelium of the body wall until they meet in the mid-ventral line in front of the first gill to form the ventral nerve cord.

Numerous tentacular nerves (Fig. 41, T.N.) arise separately from the brain. Hessle (1917) considers this condition to be secondary and due to the division of two main nerves at their origin from the brain.

The nerves to the dorsal lip are formed by the division of a pair of nerves from the ventral sides of the two groups of tentacular nerves, immediately after they enter the lip. These small nerves lie beneath the epithelium of the lip and are not clearly separated from it.

The nerves of the ventral lip are fewer in number, but similarly situated, and probably arise from the same pair of nerves as those of the dorsal lip.

The ventral nerve cord (Fig. 53, V.N.) runs throughout the length of the worm; there are no distinct ganglia as in *Pomatoceros* and *Sabella*. It consists of two nerve tracts separated by non-nervous tissue. Lateral nerves are given off from the ventral nerve cord throughout its length. They run immediately above the ventral epithelium between the bands of circular muscle. Some of these supply the chaetal muscles and others end on the muscles of the body wall.

[*The brain and oesophageal connectives must be studied from sections. The ventral nerve cord and segmental nerves are best seen by pinning out a worm, which has previously been opened in the usual way from the dorsal surface, with the ventral side uppermost, and gently removing the epithelium with a needle. A worm which has been dissected the previous day and left in water overnight provides good material.*]

The Excretory and Reproductive Systems

[*To expose the nephridia cut through the layer of oblique muscles near their attachment at the mid-lateral and mid-ventral lines, in the* *anterior thoracic region of the body. The gonads can be seen at the anterior end of the posterior chamber, among the ventral glands.*]

The excretory and reproductive systems of *Amphitrite* consist of numerous pairs of nephridia, probably representing nephromixia as in the Sabelliformia. Their structure has been described by Meyer (1887) for *A. rubra.*

The nephridia occur in two distinct series :—

i. Three anterior pairs with their internal openings in front of the diaphragm; these must be purely excretory in function, as the sex cells develop only behind the diaphragm.

ii. Ten or eleven posterior pairs, opening internally behind the diaphragm, which perform both excretory and reproductive functions, unlike the gonoducts of the Sabelliformia.

Each nephridium has essentially the same parts as in *Pomatoceros.* The funnel, which opens into the coelom, is attached to the body wall in the lateral line, and consists of fimbriated dorsal and ventral lips (Fig. 51, D.L.F., V.L.F.), the furrows on the dorsal lip being closer together than those on the ventral. This funnel leads by means of a narrow tube into a much wider excretory sac (Fig. 51, EX.S.) bent on itself to form a V, the outer limb of which leads by a short duct (Fig. 51, EX.D.) to the external opening already described (p. 61). The excretory sacs of the three anterior pairs of nephridia and of the first few posterior ones are longer than those of the remainder : those of the third pair lie entirely in the posterior body chamber, and their funnels are situated between the body wall and the diaphragm. The two limbs of the excretory sac are enclosed in the same covering of coelomic epithelium. They differ in colour, however, the inner being orange, and the outer cream.

In transverse section the sacs differ from those of *Sabella* and *Pomatoceros* chiefly in the presence of numerous large spaces within their walls ; these can be seen as clear vacuoles in fresh material and probably contain excretory fluid (Fig. 52, EX.F.) (Meyer, 1887). The cells, which contain darkly staining excretory granules (Fig. 52, EX.G.), bear a brush border in which the rods (Fig. 52, R.) are much more distinct than in *Pomatoceros*. Among them are a few very long cilia (Fig. 52, C.) which can be seen beating vigorously in living cells.

Since no blood vessels go to the excretory sacs, excretory material must be brought to the nephridia from the coelomic fluid. This may be brought about by the cilia on the funnels creating currents to draw the fluid in, or, since the sacs are only separated from the coelom by the peritoneum, soluble waste material can probably be absorbed directly through this.

The sexes are separate as in the Sabelliformia. At Plymouth breeding appears to take place in the spring (M.B.A., 1931).

The gonads (Fig. 53, GON.) are situated in a few of the anterior segments of the posterior chamber and project into the coelom as small bodies intermingled with the ventral glands. They appear to be formed from the coelomic epithelium surrounding the ventral blood vessel, but their true origin may be the same as in the Serpulids (p. 41).

Scott (1911) working on an unnamed species of *Amphitrite* found that coelomic corpuscles and unripe eggs were prevented from entering the nephridia, only ripe eggs being allowed to enter. This selection is brought about by the cilia on the grooves of the funnel exercising a sorting action on bodies of different shapes and specific gravities. The mechanism would apparently have to be reversed to enable sperms to enter while rejecting coelomic corpuscles, but whether this occurs is not known. According to Scott, eggs are forced out of the external nephridial openings by the wave-like contractions of the body.

The Development

The development of *A. johnstoni* has not been described, but that of *A. ornata* was studied by Mead (1897). The following description is based on his paper.

The larva has a broad prototroch, a ventral neurotroch and a band of cilia round the posterior region in addition to a tuft of long cilia at each end. Its ciliation, therefore, closely resembles that of *Pomatoceros*. Two eyespots are visible and at the anterior end are five spherical bodies, probably vesicles, which from their position might correspond to the head vesicles of *Pomatoceros* and *Sabella.* When the larva has developed about five trunk segments, it sinks to the bottom. Here it becomes modified for a less active life and loses all its surface ciliated tracts.

GENERAL CONCLUSIONS.

Pomatoceros, Sabella and *Amphitrite* all show modifications for a tubicolous mode of life, but the first two are the more completely adapted to this existence. The main differences between *Pomatoceros* and *Sabella* and indeed between Serpulids and Sabellids in general can be attributed partly to their different methods of tube formation, since all the former and none of the latter have a calcareous tube, and partly to the usually larger size of the latter. The differences between these two genera and *Amphitrite* or, more generally, the Terebellids, are due to the burrowing habits and temporary tubes of the latter in contrast to the more permanent ones of the former.

The reduction of parapodia in all three families is correlated with their sedentary existence. The uncini appear to be developed in connection with a tube-dwelling existence, and *Amphitrite,* being less adapted to this than the other two genera, has them only at the anterior end.

The presence of a thoracic membrane in almost all Serpulids and no Sabellids may be due to the possibility of circulating water in the tube by ciliary currents in the former smaller worms, while in the latter larger ones it may be impracticable, or a pumping action may be more easily set up in the less rigid tubes of the latter. Until more is known of the respiratory currents in the Serpulids, the explanation of the membrane must remain uncertain.

The larger size of the Sabellids also explains the necessity for a skeleton to support the branches of the branchial crown and to give attachment to the larger muscles working it. The greater development of the ventral longitudinal muscles in *Sabella* may have become possible with the development of a skeleton on which they could be inserted.

The appendages of the prostomium have become modified in all three families to form organs which are largely concerned in collecting food. In *Amphitrite* the tentacles creep over the surface of the mud and thus come into direct contact with the food and special current-creating cilia to bring food to them are unnecessary. Since the Sabelliformia are sedentary animals and their branchial filaments are non-extensile structures, some method of creating a current of water to bring food to them must be used. This current is formed by the latero-frontal cilia in Serpulids and by these and the abfrontal cilia in Sabellids. No satisfactory explanation has been found for the existence of an extra set of cilia in the latter.

The greater development of the branchial folds in *Sabella* than in *Pomatoceros* and the consequent provision of a sorting mechanism is occasioned by the elaborate method of tube formation. Such a method is not however present in all Sabellids (Nicol, 1930).

The difference between the method of food-collecting in *Pomatoceros* and *Sabella* on the one hand, and in *Amphitrite* on the other, accounts in part for the difference in the structure of the alimentary canal. The food of the two former is restricted to particles in suspension in the water, while that of the latter can include larger particles from the substratum, necessitating the muscular posterior region of the stomach, which probably functions as a gizzard.

Since the tubes of the Sabelliformia are permanent it is necessary that they should be prevented from becoming fouled by waste matter. This is accomplished in two ways—firstly, by the presence of mucous glands in the posterior end of the gut and in the body wall around the anus, ensuring that the faeces become entangled in mucus, and the provision of a groove to take this mucous string to the anterior end of the worm ; secondly, by the restriction of the nephridia to a single pair which opens anteriorly in such a position that their excreta will be carried forward by the outgoing current of water between the filaments of the branchial crown. The restriction of the nephridia to a limited number of anterior segments in *Amphitrite* will likewise tend to prevent excretory products accumulating behind the worm.

No explanation has been found for the occurrence of blind-ending vessels in the Serpulidae and Sabellidae. It is interesting to note however that in the Chlorhaemidae, the only other family of Annelids which possess chlorocruorin as their blood pigment (Fox, 1926), blind-ending vessels also supply the two large "palps" (Johannson, 1927).

The opening of the gonoducts near the ventral groove in *Pomatoceros* and the provision of ciliated grooves leading from them to the same groove in *Sabella* enables the sex products to be carried to the opening of the tube.

The large size of the giant nerve fibres in the Sabelliformia may be due to their tubicolous habits, where a rapid contraction of the longitudinal muscles to enable the worm to regain the shelter of its tube, is advantageous. They are however absent in some tube-dwelling forms such as *Amphitrite* and present, but not so well developed, in many errant Polychaetes.

It can thus be seen that many of the peculiarities of these three worms, and especially of *Pomatoceros* and *Sabella,* may be correlated with their specialised mode of life.

LITERATURE

General (external anatomy, etc.).
Numbers 17, 26, 27, 28, 30, 37, 39, 41, 42, 43, 48, 59, 61, 62, 69.

Tubes.
Numbers 10, 12, 21, 37, 45, 54.

Anatomy.
Numbers 1, 8, 9, 11, 14, 18, 23, 25, 26, 28, 29, 31, 41, 42, 45, 46, 47, 50, 51, 52, 53, 58, 59, 61, 64, 65.

Physiology (including feeding).
Numbers 1, 2, 3, 4, 5, 6, 8, 14, 16, 19, 20, 21, 22, 24, 28, 38, 45, 59, 62, 63, 66, 68, 70.

Histology.
Numbers 7, 13, 15, 32, 36, 38, 44, 45, 50, 68.

Reproduction, Development and Regeneration.
Numbers 3, 33, 34, 35, 40, 41, 42, 49, 55, 56, 57, 60, 67, 69.

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DESCRIPTION OF PLATES

REFERENCE LETTERS

A. = Anus.
A.C. = Anterior commissure.
A.G. = Anterior ganglion.
A.INT. = Anterior intestine.
A.N. = Anterior nerve.
A.O. = Apical organ.
A.OP.M. = Accessory opercular muscle.
A.ST. = Anterior stomach.
A.V. = Anal vesicle.
AB.BR. = Abdominal bristle.
AB.UN. = Abdominal uncinus.

B. = Brain.
B.BR.V. = Basal branchial vessel.
B.G. = Basal granule.
B.GR. = Groove in brain.
B.MB. = Basement membrane.
B.V. = Blood vessel.
B.W. = Body wall.
BR.F. = Branchial filament.
BR.M. = Branchial muscle.
BR.N. = Branchial nerve.
BR.V. = Branchial vessel.

C. = Cilia.
C.EX.T. = Ciliated excretory tube.
C.F. = Ciliated funnel.
C.G. = Ciliated groove.
C.M. = Circular muscle.
C.N. = Collar nerve.
CG.T. = Chloragogenous tissue.
COE. = Coelom.
CT. = Connective tissue.
CU. = Cuticle.

D. = Diaphragm.
D.C.F. = Dorsal collar fold.
D.GR. = Ciliated dorsal groove.
D.L. = Dorsal lip.
D.L.F. = Dorsal lip of funnel.
D.L.M. = Dorsal longitudinal muscle.
D.L.N. = Nerve to dorsal lip.
D.M. = Dorsal mesentery.
D.P. = Dorsal pit.
D.R.C. = Dorsal root of oesophageal connective.
D.R.V. = Dorsal ring vessel.
D.S. = Diaphragm sac.
D.S.M. = Dorsal suspensory muscle.
D.V. = Dorsal vessel.

E.BR.M. = External branchial muscle.
E.BR.N. = External branchial nerve.
E.BR.T. = External branchial nerve trunk.
EP. = Epithelium.
EX.D. = Excretory duct.
EX.F. = Excretory fluid.
EX.G. = Excretory granule.
EX.P. = External opening of excretory duct.
EX.S. = Excretory sac.
EY. = Eyespot.

F.C. = Frontal cilia.
FE.C. = Feeding cilia.

G. = Ganglion of ventral nerve cord.
G.C. = Gland cell.
G.F. = Giant fibre.
G.S. = Gut sinus.
GL. = Gill.
GON. = Gonad.

H.V. = Head vesicle.

I.BR.M. = Internal branchial muscle.
I.BR.N. = Internal branchial nerve.
I.BR.T. = Internal branchial nerve trunk.
INT. = Intestine.

L. = Lappet.
L.C.F. = Lateral collar fold.
L.F.C. = Latero-frontal cilia.
L.L. = Lateral lip.
L.LB. = Lateral lobe.
L.M. = Longitudinal muscle.
L.M.F. = Longitudinal muscle fibre.
L.P. = Lateral process of peduncle.
L.S.N. = Nerve to lateral sense organ.
L.V. = Lateral vessel.

M. = Membrane uniting bases of branchial filaments.
M.D.L.M. = Median dorsal longitudinal muscle.
M.D.N. = Median dorsal nerve.
ME. =
M.EX.D. = Median excretory duct.
M.F. = Muscle fibre.
M.G. = Mucous gland.
M.V.L.M. = Median ventral longitudinal muscle.
MB. = Membrane covering posterior stomach.
ME. = Mesoderm.
MT. = Metatroch.
MTH. = Mouth.

N. = Nucleus.
N.C. = Nerve cord.
NOT. = Notopodium.
NP. = Neuropodium.
NT. = Neurotroch.

O. = Ovum.
O.BR.M. = Oblique branchial muscle.
O.BR.N. = Oblique branchial nerve.
O.OD. = Opening of oviduct.
OB.M. = Oblique muscle.
OD. = Oviduct.
OES. = Oesophagus.
OP. = Operculum.
OP.M. = Opercular muscle.
OP.N. = Opercular nerve.

P.C. = Posterior commissure.
P.F. = Parallel fold.
P.G. = Posterior ganglion.
P.INT. = Posterior intestine.
P.N. = Nerve to palp.
P.ST. = Posterior stomach.
P.T.M. = Posterior transverse muscle.
P.V. = Pinnule vessel.
PD. = Peduncle.
PE. = Peritoneum.
PER. = Peristomium.
PERF. = Perforation.
PH. = Pharynx.
PP. = Palp.
PR. = Prostomium.
PRN. = Protonephridium.
PT. = Prototroch.

R. = Rod.
R.V. = Ring vessel.

S.G. = Sub-oesophageal ganglion.
S.I.V. = Sub-intestinal vessel.
S.N. = Segmental nerve.
S.O.C. = Sub-oesophageal commissure.
SEP. = Septum.
SK.AX. = Skeletal axis.
SK.P. = Skeleton of palp.
SK.S. = Skeletal sheath.
ST. = Stomach.

T. = Tentacle.
T.C. = Transverse commissure.
T.N. = Tentacular nerve.
TH.BR. = Thoracic bristle.
TH.M. = Thoracic membrane.
TH.M.N. = Thoracic membrane nerve.
TH.M.V. = Thoracic membrane vessel.
TH.UN. = Thoracic uncinus.

UN. = Uncinus.

V.C.F. = Ventral collar fold.
V.C.G. = Ventral ciliated groove.
V.G. = Ventral groove of intestine.
V.GL. = Ventral gland.
V.L. = Ventral lip.
V.L.F. = Ventral lip of funnel.
V.L.M. = Ventral longitudinal muscle.
V.L.N. = Nerve to ventral lip.
V.M. = Ventral mesentery.
V.N. = Ventral nerve cord.
V.R.C. = Ventral root of oesophageal connective.
V.R.V. = Ventral ring vessel.
V.S. = Ventral sac.
V.SH. = Ventral gland shield.
V.S.M. = Ventral suspensory muscle.
V.T. = Vacuolated tissue.
V.T.L.M. = Ventral thoracic longitudinal muscle.
V.V. = Ventral vessel.

Small numerals in the Figures indicate the number of the segment.

DESCRIPTION OF PLATES

POMATOCEROS TRIQUETER.

PLATE I.

Fig. 1. A tube seen from above. × 2.
Fig. 2. Transverse section of a tube to show the perforations. × 6.
Fig. 3. Section of a tube near its attached surface, taken parallel to the substratum, to show the same. × 6.
Fig. 4. Inside view of the calcareous plate sometimes found at the posterior end of a tube. × 14.
Fig. 5. Anterior end of the worm seen from the right side. Only the base of the branchial crown is shown. × 19.

PLATE II.

Figs. 6 and 7. Two different types of opercula with the distal ends of their peduncles. × 19.
Fig. 8. Somewhat diagrammatic transverse section of a branchial filament, taken between the origin of two pinnules. × 200.
Fig. 9. Transverse section of a pinnule. × 690.
Fig. 10. Transverse section of a palp. × 420.
Fig. 11. Uncinus from a thoracic neuropodium. × 970.
Fig. 12. Distal end of one of the first group of thoracic bristles. × 140.
Fig. 13. Distal end of a bristle from one of the posterior thoracic notopodia. × 150.
Fig. 14. Tip of the same bristle. × 490.
Fig. 15. The same seen from the dorsal side of the worm. × 330.
Fig. 16. Distal end of a bristle from one of the abdominal notopodia. × 625.

PLATE III.

Fig. 17. Diagram of the muscles of the anterior end of the body seen from above ; drawn from a reconstruction. × 50.

Fig. 18. Somewhat diagrammatic longitudinal section through the anterior end. The dorsal and ventral mesenteries have been omitted. × 53.

PLATE IV.

Fig. 19. Slightly oblique transverse section at the level of the brain ; viewed from the front. The base of the ventral collar lobe is seen on the right-hand side only. The central fibrous part of the brain is lined, that occupied by the nerve cells dotted. × 66.

Fig. 20. Transverse section through the abdomen of a mature female. The oviduct and coelom contain numerous ripe ova, and there is a group of smaller unripe ones on the left. × 51.

PLATE V.

Fig. 21. Part of a transverse section through the stomach. × 600.

Fig. 22. Part of a transverse section through the intestine. × 720.

Fig. 23. Diagram of the excretory organs seen from the ventral side ; drawn from a reconstruction. × 36.

Fig. 24. Part of a transverse section through the excretory sac of a nephridium. × 450.

Fig. 25. Section through a ring vessel showing the chloragogenous tissue. × 890.

PLATE VI.

Fig. 26. Diagram of the anterior part of the nervous system seen from above ; drawn from a reconstruction. × 60.

Fig. 27. Posterior view of the brain drawn from the same reconstruction. The ventral nerve cords and median dorsal nerve are shown in section. × 68.

PLATE VII.

Fig. 28. Part of a transverse section to show the structure of the lateral sense organ. Only the opening of the duct is shown, the rest being posterior to the line of section. × 165.

Fig. 29. Lateral view of an advanced trochosphere about 6 days old. (From Segrove.) × 290.

SABELLA PAVONINA.

Fig. 30. Anterior end seen from the right side and slightly from below. Only the base of the branchial crown is shown. × 8.

PLATE VIII.

Fig. 31. Inside view of the branchial crown spread open. Only the bases of the filaments are shown. × 9.

Fig. 32. Diagram of the muscles at the anterior end of the body seen from below to show their attachment to the skeleton ; drawn from a reconstruction. × 30.

PLATE IX.

Fig. 33. Uncinus from a thoracic neuropodium. × 415.

Fig. 34. Distal end of a paddle-shaped bristle accompanying a thoracic uncinus. × 145.

Fig. 35. Distal end of one of the dorsal row of bristles from a thoracic notopodium. × 210.

Fig. 36. Distal end of a bristle from an abdominal neuropodium. × 210.

Fig. 37. Transverse section of a branchial filament at the level of the basal folds to show the position of the skeleton and the variation in height of the epithelium. × 125.

Fig. 38. Transverse section through the body just anterior to the brain. × 44.

Fig. 39. Dorsal view of the nerve cords and segmental nerves in a small region of the abdomen. × 40.

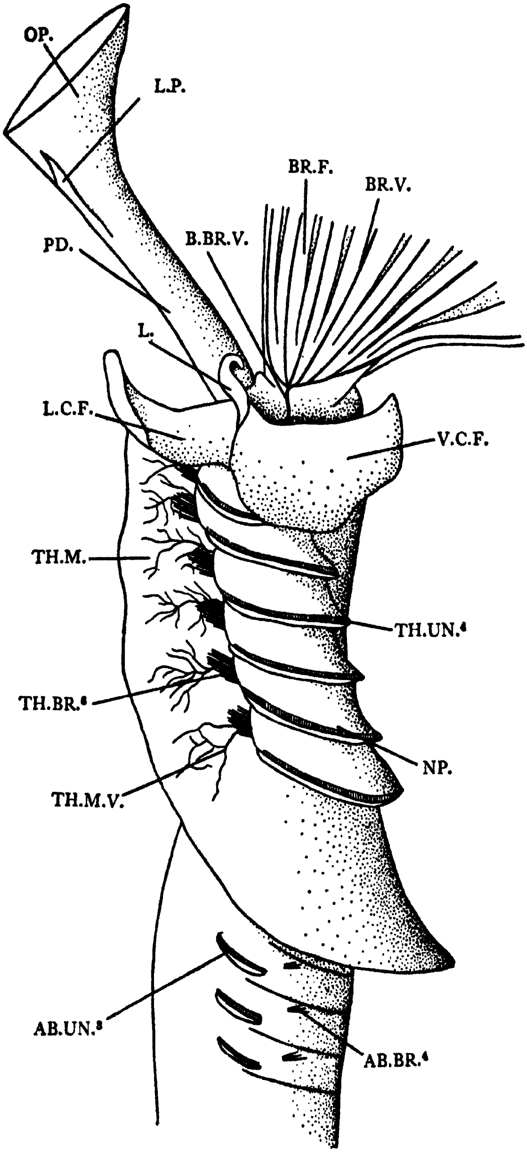
AMPHITRITE JOHNSTONI.

PLATE X.

Fig. 40. Anterior end seen from the right side. Only the bases of the tentacles are shown. × 3.
Fig. 41. Diagrammatic transverse section of a tentacle. × 145.
Fig. 42. Diagrammatic transverse section of one of the branches of a gill. × 125.
Fig. 43. Uncinus from a thoracic neuropodium. × 170
Fig. 44. Distal end of one of the posterior row of bristles from a thoracic notopodium. × 450.
Fig. 45. Distal end of one of the anterior row of the same. × 150.
Fig. 46. Transverse section of the oesophagus. × 25.
Fig. 47. Transverse section through the body in the region of the posterior intestine. × 14.
Fig. 48. Part of a transverse section of the posterior stomach. × 110.

PLATE XI.

Fig. 49a & Fig. 49b. Dorsal view of a dissection of the alimentary canal; the posterior stomach and part of the anterior intestine have been turned to the right. The numbers indicate segments. × 1·5.
Fig. 50. Transverse section of the dorsal blood vessel to illustrate the position of the heart body, which is stippled: the lumen is black. × 35.
Fig. 51. Posterior nephridium seen from above. × 5.
Fig. 52. Part of a transverse section through the excretory sac of a posterior nephridium. × 280.
Fig. 53. Part of a transverse section through the body wall in the thoracic region of a worm with well-developed gonads. × 27.



J.G.T. del.

FIG. 5.

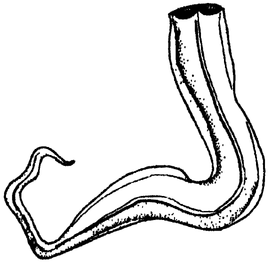


FIG. 1.

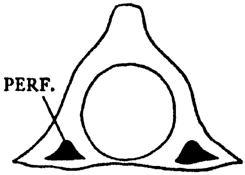


FIG. 2.

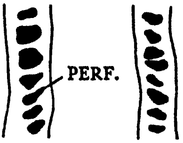


FIG. 3.

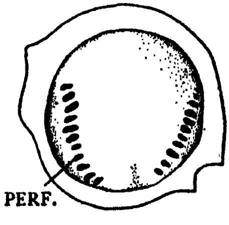


FIG. 4.

POMATOCEROS

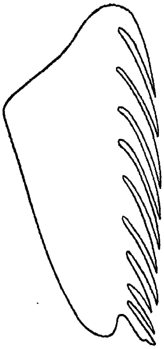


Fig. 11.

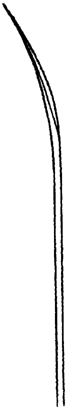


Fig. 12.

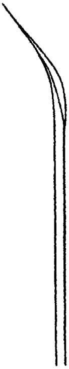


Fig. 13.

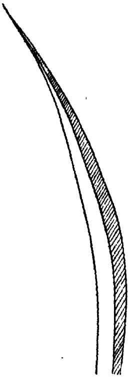


Fig. 14.

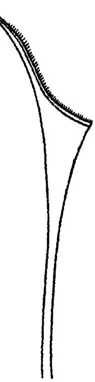


Fig. 16.

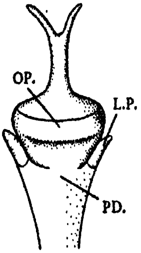
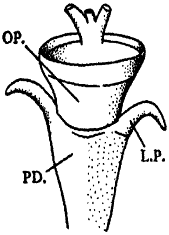


Fig. 6.



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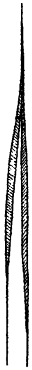

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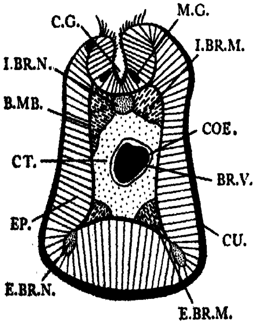
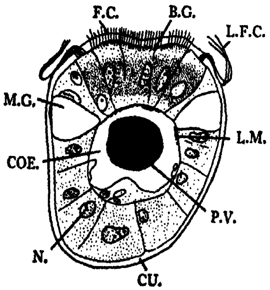


J.G.T. del.

Fig. 8.



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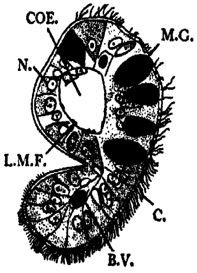


Fig. 10.

POMATOCEROS

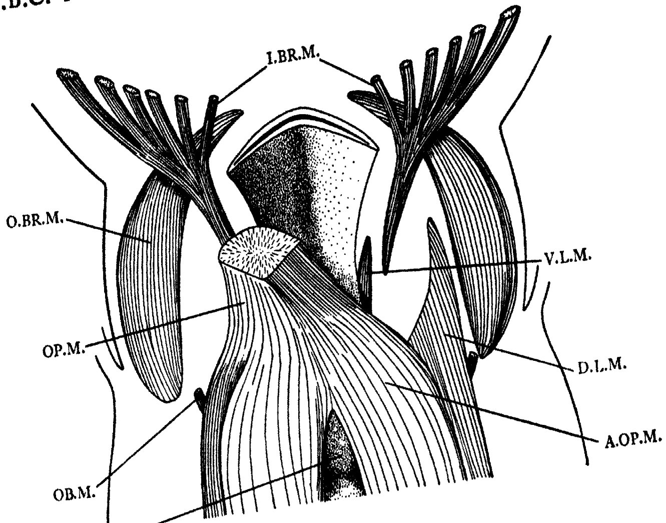


FIG. 17.

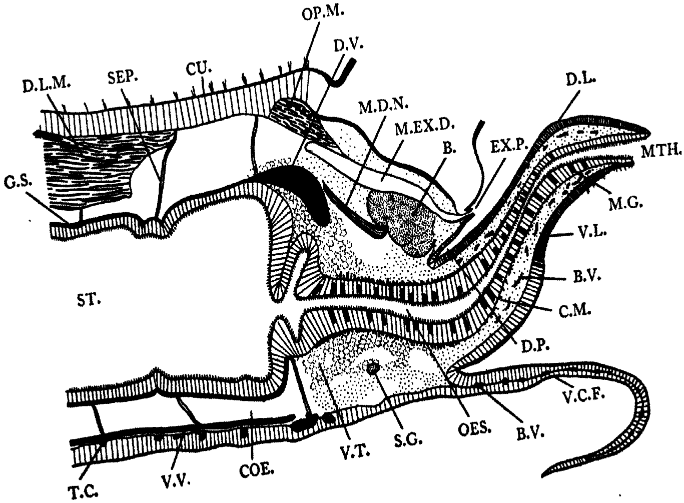


FIG. 18.

J.G.T. del.

POMATOCEROS

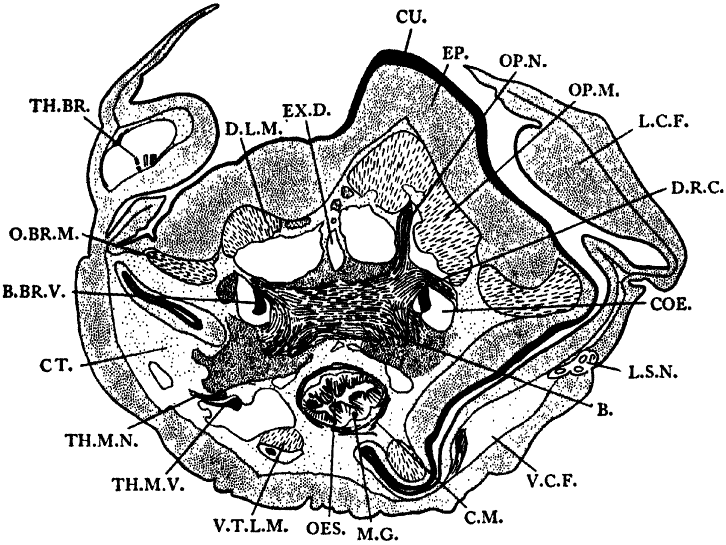
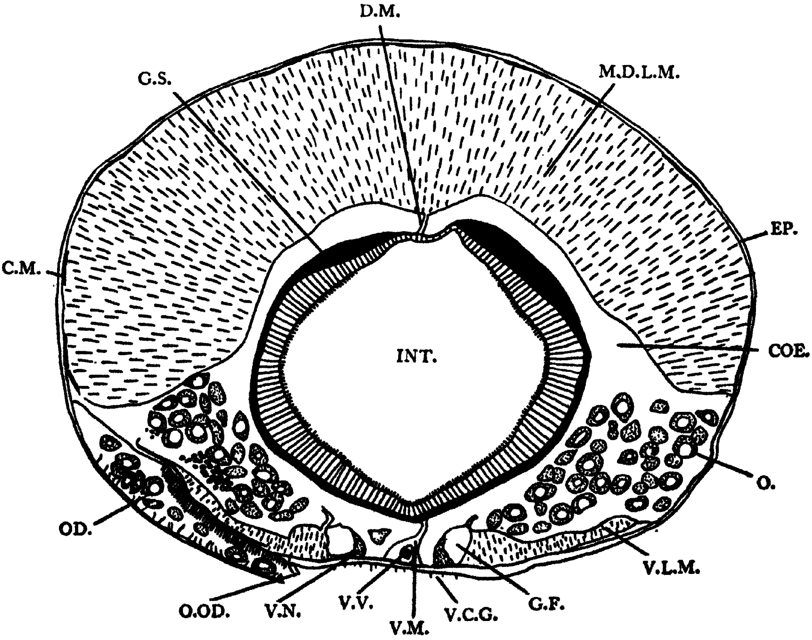


Fig. 19.



J.G.T. del.

Fig. 20.

POMATOCEROS

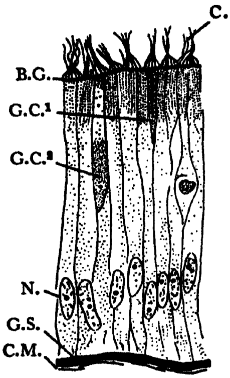


FIG. 21.

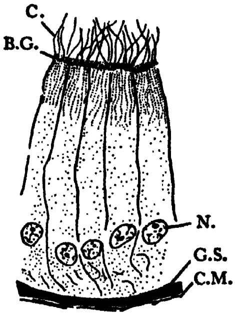


FIG. 22.

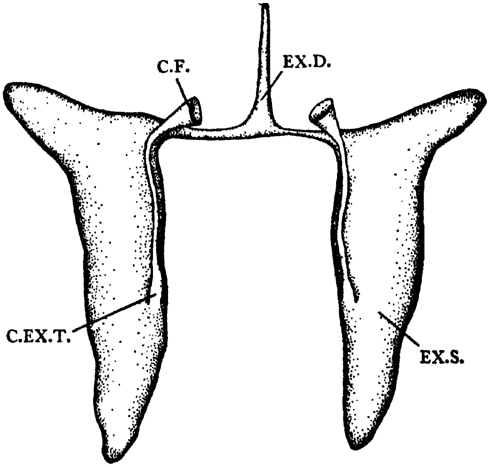
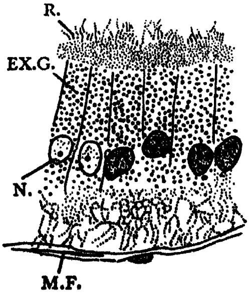


FIG. 23.



J.G.T. del.

FIG. 24.

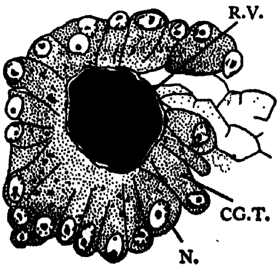


FIG. 25.

POMATOCEROS

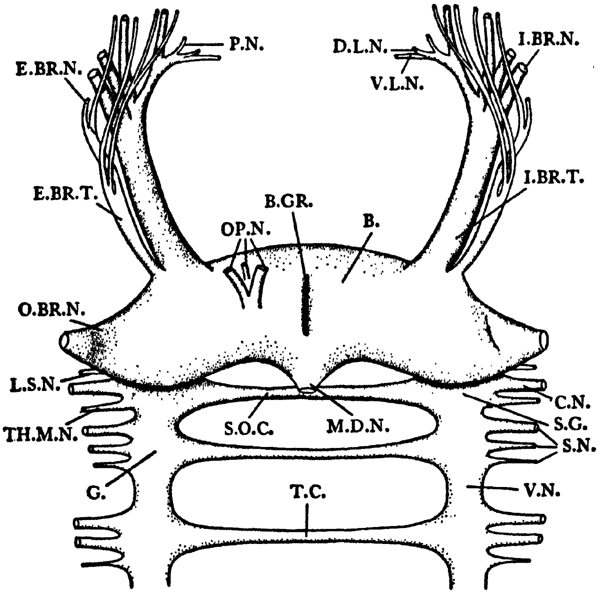
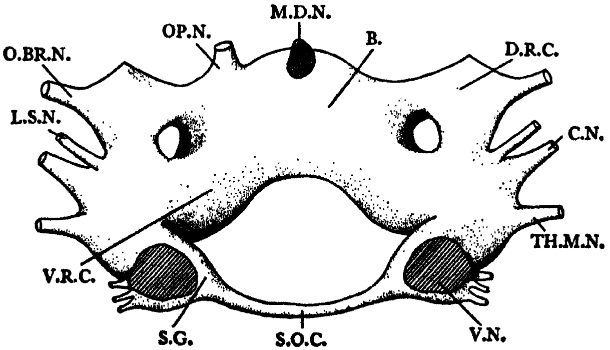


FIG. 26.



J.G.T. del.

FIG. 27.

POMATOCEROS

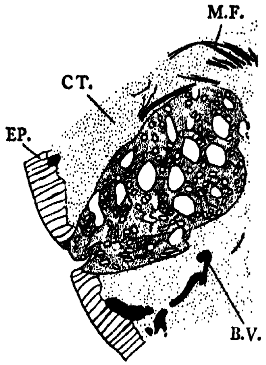


Fig. 28.

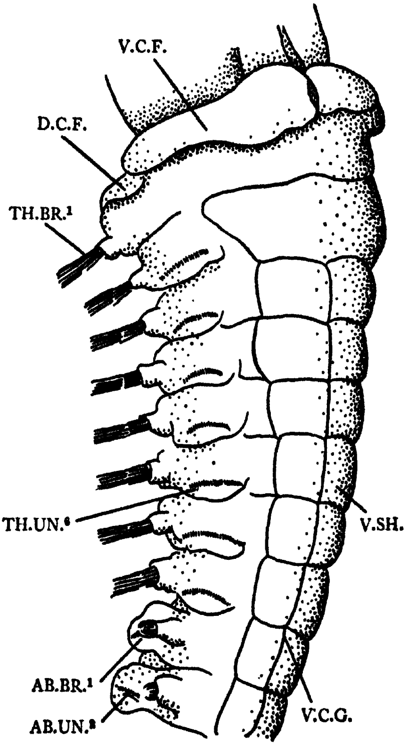
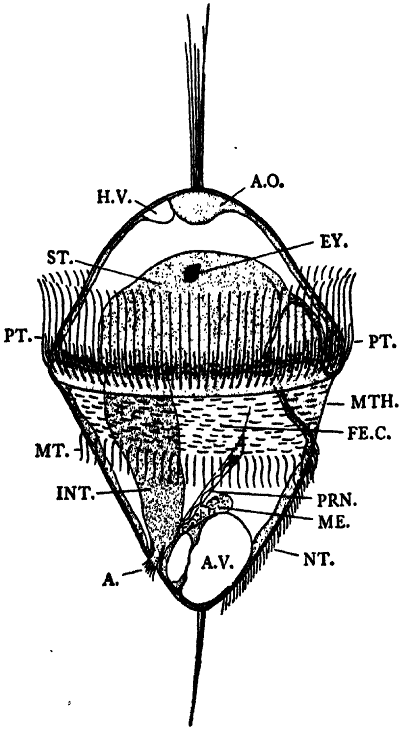


Fig. 30.



J.G.T. del.

Fig. 29.

POMATOCEROS (Figs. 28, 29)
SABELLA (Fig. 30)

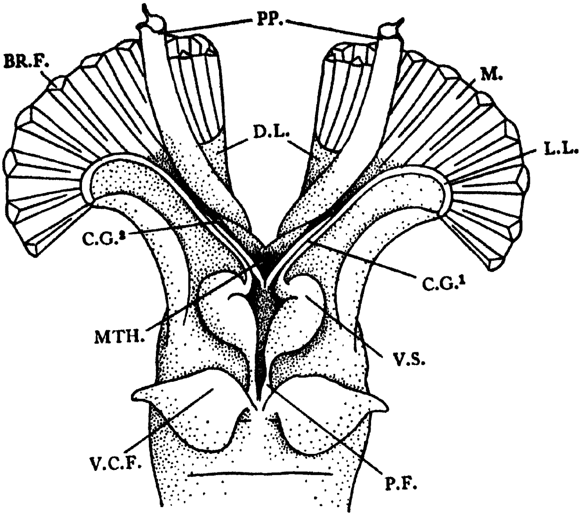


FIG. 31.

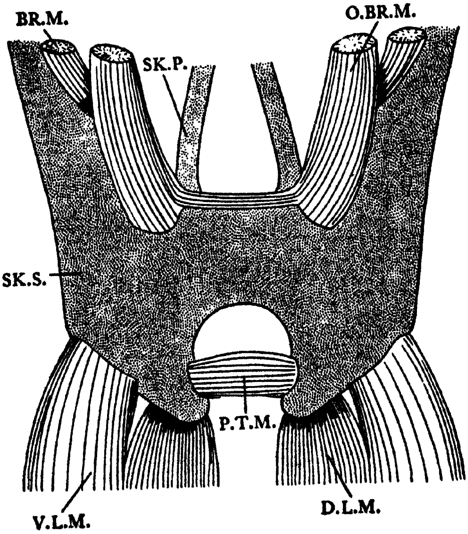


FIG. 32.

SABELLA

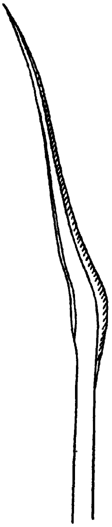


FIG. 36.

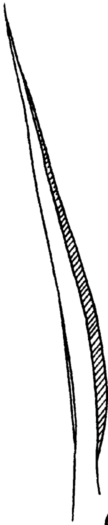


FIG. 35.

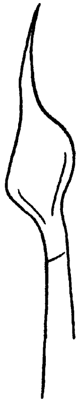


FIG. 34.

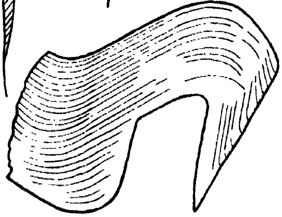


FIG. 33.

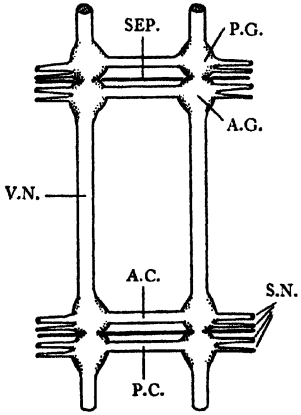
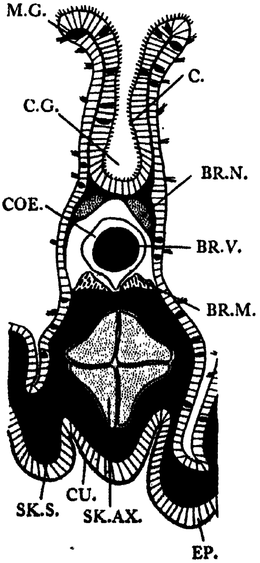


FIG. 39.



J.G.T. del.

FIG. 37.

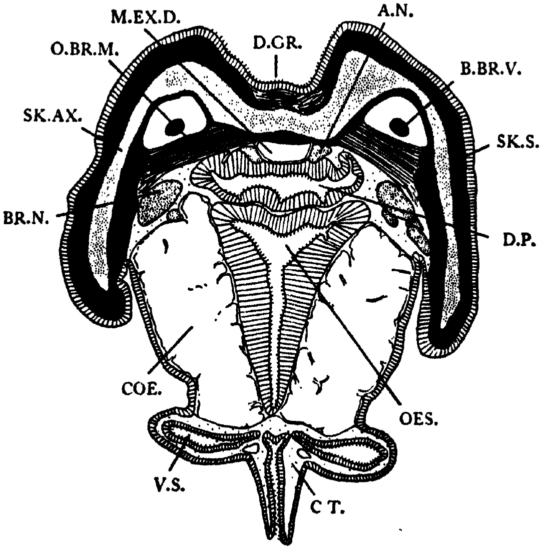


FIG. 38.

SABELLA

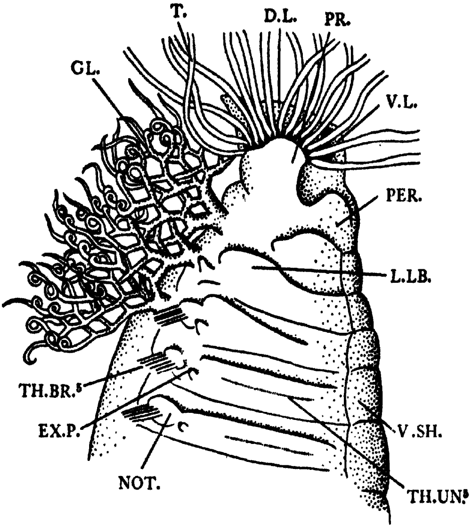


FIG. 40.

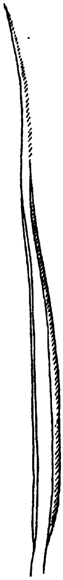
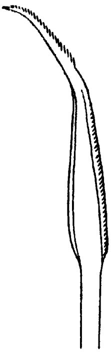


FIG. 44.



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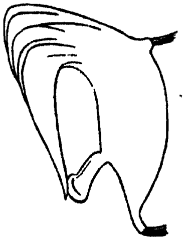

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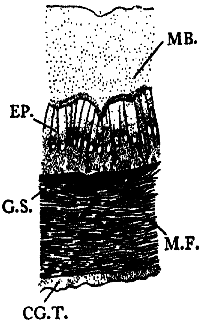

FIG. 48.

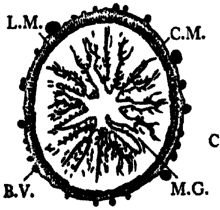

FIG. 46.

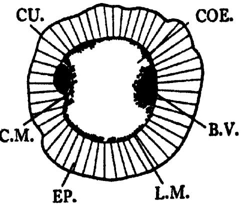

FIG. 42.

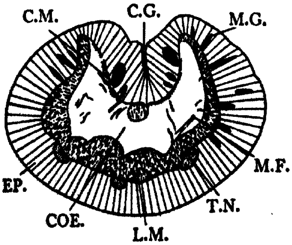

FIG. 41.

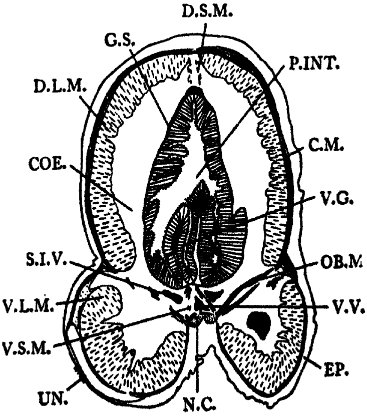

FIG. 47.

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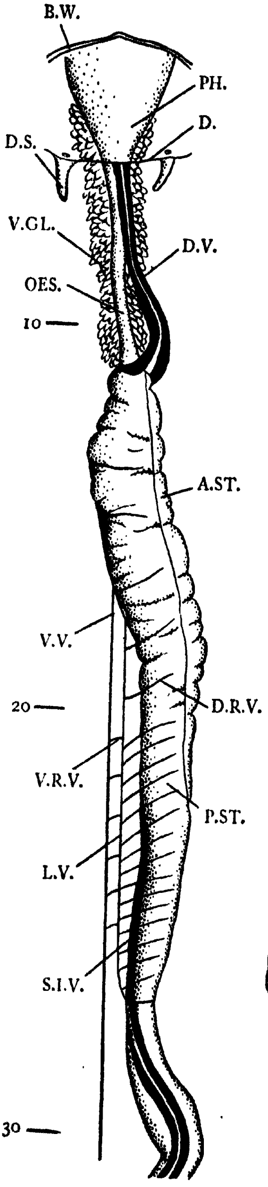
AMPHITRITE



J.G.T. del.

Fig. 49a

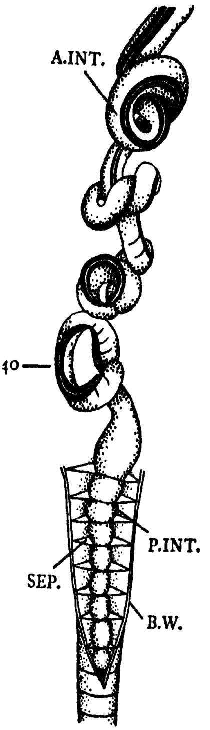


Fig. 49b.

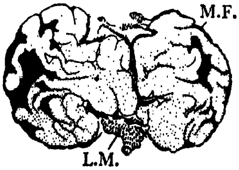


Fig. 50.

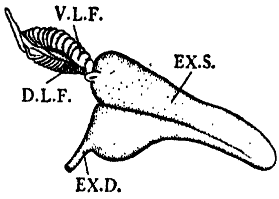
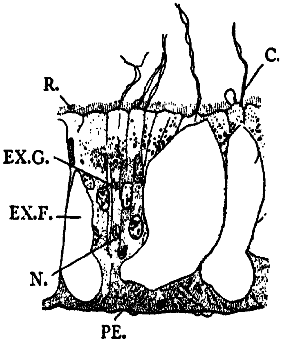


Fig. 51.



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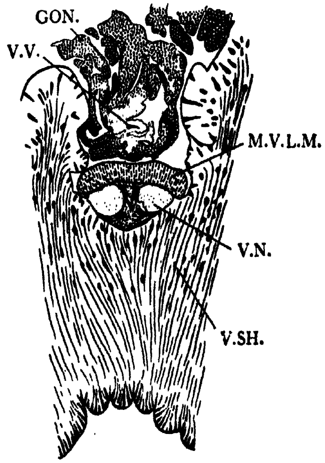

Fig. 53.

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